THE TAPHONOMY OF BIRDS

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ABSTRACT

Palaeo-ornithology has been dominated by taxonomy. To try and redress the balance and help palaeoecologists interpret fossil birds in a biological and ecological perspective, the taphonomy of birds needs to be fully understood. The taphonomy of birds is concerned with all processes from death to the collection of the fossil bird. Between these two points (the transfer of the organism from the biosphere to the lithosphere) a variety of forces and processes affect the bird/fossil. By means of experiments in the natural environment and in controlled conditions in the laboratory, and subsequent comparisons of the results with case studies of fossil assemblages, the processes leading to preservation can be deduced and the former living community restored on the basis of the fossil evidence.

The research involved two main approaches: 1. experimental taphonomy / observational taphonomy; and 2. case histories of fossil communities and their interpretation.

Experimental work was carried out in the natural environment. Two field sites were chosen in southern Florida, a freshwater environment and a marine environment. The monitoring and controlling of these experiments required knowledge and techniques in zoology, botany, ecology, sedimentology, limnology, marine biology, microbiology, pathology and forensic science. Results obtained included the effects of scavenging, anoxia, transport, rate of burial, and temperature on rates of decay, the causes of bird mortality, the processes resulting in disarticulation, and the effects of decay upon feathers.

Once the experimental/observational data had been collected they allowed a series of taphonomic thresholds (a decay sequence) to be defined. These data were then applied to case studies of fossil bird assemblages from different sedimentological environments. The following Lagerstätten were investigated: Messel (Eocene, Germany) = restricted lacustrine; Green River (Eocene, USA) = lacustrine; Solnhofen Lithographic Limestone (Jurassic, Germany) = restricted marine; La Meseta Formation (Eocene, Antarctica) = marine; Rancho La Brea (Pleistocene, USA) = terrestrial "trap". The biases in each environment were assessed (e.g. birds in an aquatic terrestrial environment had a higher preservation potential than birds from a terrestrial environment).

The fossil record of birds is not as depauperate as previously thought but is heavily biased, depending on the proximity of the bird's habitat to that of the preserving sedimentary environment. Marine and littoral birds are poorly represented even though they inhabit sedimentary environments with a high preservation potential. This reflects low densities of birds per unit area. Aquatic birds (and terrestrial birds that inhabit the ecotone surrounding freshwater together with some larger forms from further away) are much better represented. This is because they inhabit the only terrestrial environments with a high preservation potential, coupled with the high densities of individuals per unit area. The bias towards large terrestrial birds is due to their large bones being more resistant to transport induced damage.

These results have implications for the understanding of the evolution of birds. Patterns of evolution in birds can not be fully resolved on fossil evidence alone; biases in the taphonomy of birds only permit a small proportion of species from certain environments to be preserved.

The taphonomy of feathers was investigated and it was discovered that the "organic trace" that commonly represents the outline of the feather trace is the diagenetically altered glycocalyx of the bacteria that were degrading the feather. In several localities these feather-degrading bacteria are preserved in authigenic minerals.

The taphonomy of bats and pterosaurs was also investigated. The similarity of anatomical structures of birds, bats and pterosaurs results in similar taphonomic pathways.

For my family.

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Author's Declaration

This thesis and the conclusions herein are the result of my own original work, except where due reference and acknowledgement has been given.

Signed.

Paul Geoffrey Davis.

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CONTENTS

Chapter One
Introduction and Previous Research.

1a. Introduction

Birds have always attracted wonder, for the simple fact that they fly. Since earliest times man has tried to emulate them (e.g. the Greek legend of Daedalus and Icarus). Man's fascination with birds has continued into his scientific endeavours, for example in the last 3.5 years there have been 6736 scientific publications on birds (data from BIDS electronic reference recovery system, June 1995). It is quite paradoxical that fossil birds have not yet been thoroughly investigated. One of the fields of palaeoornithology that has been neglected more than most is avian taphonomy.

This project aims to redress the balance of this neglect and to analyse palaeontological data in light of the recent advances in taphonomy to produce a initial platform from which further, detailed studies can be performed.

The research has followed two lines of approach. The first is observational, where actualistic data have been recorded on the taphonomy of birds by field work in different environments. The second approach is experimental. Bird specimens were allowed to decompose and disarticulate in a natural environment and environmental factors were recorded. These two approaches have been used to analyse the taphonomy of certain deposits containing fossil birds. This was completed by taphonomically examining specimens contained in museums and applying this data and also the experimental and observational data to produce taphonomic histories. The final stage was briefly to examine the fossil record of bats and pterosaurs and to see if the earlier observations are also applicable to these flying vertebrates.

The morphological terminology used in this thesis follows that of Howard (1929) and Lucas and Stettenheim (1972). The classification system used follows that of Welty and Baptista (1988).

1b. The Avian Fossil Record

The avian fossil record has long been described as poor. This view, however, has been propagated largely by workers in other fields (see Chapter 1d1.). Most palaeo-ornithologists are aware that the avian fossil record is good (Unwin 1993, pers. comm. 1994). The confusion has arisen as a result of the simple fact that a large proportion of fossil bird material consists of broken or damaged, isolated bones (see for example, Chapter 5e5.).

However, the taphonomic properties of bird bones should not be confused with the quality of the fossil record.

An exhaustive review of the avian fossil record is beyond the scope of this thesis but it is pertinent to provide here a catalogue of the most significant localities/deposits. This review serves as a guide to the sites and an introduction to the literature, especially to those localities mentioned within the text.

The following criteria were used in deciding which sites to include in Tables 1 and 2:

1. Only those Mesozoic (Table 1.1) and Tertiary (Table 1.2) sites which contain abundant, or exceptionally well preserved specimens.
2. No sites yielding only feathers, as these are exhaustively documented in Chapter 4.
3. All other sites (not covered by points 1 or 2) that are referred to in this thesis.

1c. History of Taphonomy

The science of taphonomy is still in its infancy. The term taphonomy was coined by Efremov (1940) from the Greek ταφοζ (taphos - burial) and νομοζ (nomos - laws). However, the foundations of modern taphonomic research were laid down with those of palaeontology (see Cadée, 1990). When describing fossil organisms most palaeontologists made observations and formulated theories on how the organisms might have become fossils. These early workers focused upon interpreting fossil deposits in terms of post-mortem processes that they were able to observe in the natural environment. Many of these studies were performed in Germany between the two World Wars, and included the monographic works on the studies of death, decay, disarticulation and burial of vertebrate carcasses by Weigelt (1929/1989) and Richter (1928). It was Richter (1928) who coined the term 'aktuopalaontologie' for the study of post-mortem processes on modern organisms and their relevance to the form of fossil assemblages. This concept of the present being the key to the past is known as uniformitarianism, and is still regarded as one of the key parameters in taphonomic research (see Lyman, 1994).

However, taphonomy was not recognised as a separate study until the mid and late 20th century, after the defining work of Efremov (1940). Efremov recognised that diagenetic factors, as well as biostratinomic and necrolytic effects, also bore relevance to fossil accumulations. Much of the work following this in the 1950-1970's was directed towards analysing the effects of taphonomic bias or losses in the fossil record and how to eliminate them in

palaeoecological reconstructions. This body of papers included works on terrestrial vertebrates, such as those by Olson (1952, 1958), Shotwell (1955) and Voorhies (1969, 1970).

Actualistic studies became fashionable in the late 1960-1970's especially with the onset of the ideas that taphonomy could have a potential contribution to archaeological research (Gifford, 1981). Investigations included work upon transportation (Toots, 1965; Voorhies, 1969), disarticulation (Hill, 1978, 1979a,b; Hill and Behrensmeyer, 1984, 1985), and weathering (Hill, 1976; Behrensmeyer, 1975, 1978) of modern animal skeletons (it is important to note that these studies mostly refer to large mammalian vertebrate remains). The 1950-1970's also saw the introduction of the application of statistical techniques to taphonomic investigations, including the estimates of original numbers of living organisms by Shotwell (1955), Grayson (1978) and Holtzman (1979), and the modelling of large-scale biases in the fossil record by Raup (1976, 1979) and Sepkoski (1976).

For a more comprehensive review of the early literature of taphonomic research, the reader is directed to Behrensmeyer and Kidwell (1985), Thomas (1986), Cadée (1990), and papers in Donovan (1990), Briggs and Crowther (1990) and Allison and Briggs (1991b) and, specifically for vertebrate taphonomy, Shipman (1981), Behrensmeyer and Hill (1980) and Lyman (1994).

In the past fifteen to twenty years the numbers of taphonomic studies have grown exponentially. In most cases palaeontological investigations are not considered to be complete without some mention of preservational styles and possible taphonomic histories. Indeed it was in the mid-1980's when the concept of fossils possessing a taphonomic history was first defined by Andrews and Cook (1985), although preliminary schemes were illustrated by Fagerstrom (1964) and Seilacher (1977). Taphonomic histories are now understood to be complex and cumulative, i.e. the effects of a late taphonomic process upon a fossil are often related to those which occurred early in the history. It has also been recognised that a taphonomic history may be determined by pre-mortem considerations, for example, the preference of certain habitats or diets (Shipman, 1981).

Most modern taphonomic studies focus upon the positive contributions that fossils and fossil assemblages can provide to our understanding of the biotic record, rather than being solely concerned with taphonomic losses. Seminal papers on this subject include works by Seilacher (1977), Behrensmeyer and Kidwell (1985), Thomas (1986), and Kidwell and Behrensmeyer (1988). Specific topics being researched include taphonomy's contribution to our knowledge of past ecosystems (e.g. Brett and Baird, 1986;

Kidwell and Behrensmeyer, 1988) and depositional environments (Kidwell *et al.*, 1986; Behrensmeyer and Hook, 1992), the interaction of organisms and sediments (e.g. Kidwell and Aigner, 1983; Kidwell and Jablonski, 1983; Kidwell *et al.*, 1986; Brett and Baird, 1986; Brandt, 1989; Kidwell, 1991), time-averaging and relative rates of sedimentation (Behrensmeyer and Schindel, 1983; Kidwell and Bosence, 1991) and processes of fossilisation (papers in Allison and Briggs, 1991b).

Many modern taphonomic studies rely heavily upon actualistic observational, experimental and analytical approaches. They also incorporate sedimentological and stratigraphic data, providing information upon depositional environment and burial profiles. Experimental studies have included analyses of mechanical rounding and sorting by transport in simulated fluvial or marine conditions (e.g. Voorhies, 1969; Wolff, 1973; Behrensmeyer, 1975, 1991; Hanson, 1980; Shipman, 1981; Allen, 1984, 1991; Argast *et al.*, 1987; Spicer, 1991). Other studies have included observations on decay of organisms under strict laboratory or closely monitored natural conditions (e.g. Dodson, 1973; Hill, 1979b; Andrews and Cook, 1985). There has been a plethora of taphonomic theories based upon observations of hard-part modification by predation and scavenging (e.g. Dodson and Wexlar, 1979; Hill, 1979a; Haynes, 1980a,b, 1982; Fisher, 1981; Andrews and Nesbit-Evans, 1983), biogenic corrosion (Brett and Baird, 1986; Brett, 1990), and the effects of weathering (Behrensmeyer, 1975; Korth, 1979) and trampling (Behrensmeyer *et al.*, 1986; Fiorillo, 1984, 1988a,b, 1989). Some of these studies (e.g. Fisher, 1981; Fiorillo, 1989) have incorporated experimental investigations in order to demonstrate the processes leading to the formation of fossil concentrations. Understanding the processes of post-burial modification and eventual fossilisation has become a major theme of research in the 1990's, with experimental techniques being pioneered in understanding processes such as phosphatisation (e.g. Lucas and Prevot, 1991, Briggs *et al.*, 1993, Kear *et al.*, 1995), pyritisation (e.g. Canfield and Raiswell, 1991b), charring (e.g. Cope, 1980), and calcification (Canfield and Raiswell, 1991a, Briggs and Kear, 1993, 1994) of organisms.

The scope of some of these studies is often quite limited, taxonomically or in terms of the variables used to define a certain taphonomic parameter, and they can be rather simplistic in the application of results from laboratory or controlled experiments to the fossil record. For instance, much of the research concerning standardisation of disarticulation, transport and abrasion of vertebrate remains in fluvial regimes was carried out upon large mammalian skeletons and cannot be applied readily to accumulations of extinct non-mammalian microvertebrates. Other studies rely heavily upon

uniformitarianism. For example, understanding and recognition of modern predator activity is extremely useful, but how relevant is it to extinct faunas? The concepts and problems in applying actualistic procedures are further discussed and reviewed by Gifford (1981) and Lyman (1994).

1d. Previous Research

1d1 Introduction

The study of fossil birds has long been plagued by problems. The reasons for this are, at least, twofold (Olson, 1985, p. 80):

1. Insufficiency of qualified workers.
2. The trend among authors to reiterate the idea that bird bones are hollow and light and therefore are seldom preserved, thus supposedly contributing to a meagre fossil record for the class (e.g. MacFadden, 1992). Because such an introduction relieves a writer of the need to determine what actually is known about the fossil record of birds and of saying anything intelligent about the matter, such prefatory comments are unlikely to suffer the rapid quietus they deserve.

Palaeo-ornithology has been dominated by taxonomy. Unfortunately this has led to little more than taxonomic 'stamp collecting'. There has been little attempt to try to understand the fossils in a biological context. So far, these papers contain only passing comments on taphonomy. Wetmore (1944), for instance, gave the following taphonomic data as anecdotal facts within the introduction, description and conclusion of his paper:

> ..... Skulls of birds in a fossil state are rare, so that most of our knowledge of the extinct avifaunas of the World comes from wing and leg bones (p.57);
> ..... the specimen was embedded in a relatively fine sandstone that was fairly soft in character, in the upper part of the Washakie Formation of the Upper Eocene. The skeleton apparently had been overturned in some way before becoming finally embedded prior to fossilisation, since the under sides of several bones are mechanically fractured (p. 57);
> ..... The presence of these parts of the tongue (the two basi-branchials) is unusual as they have seldom been found in fossil birds (p. 61).

From the taxonomic description it is evident that an almost complete skeleton is represented with at least one element of each part of the skeleton present. It can also be deduced from the description of the bones that distortion and fracturing of the bones were due to burial compaction. From the analysis of taphonomic data and skeletal evidence the reconstruction of the bird's ecology is possible. It is shown to be a terrestrial vulture which

inhabited the shoreline of lakes and the banks of rivers, and which fed upon fish.

1d2 Observational Taphonomy

Schäfer (1972) noted that the numbers of species of birds in the fossil record is not as small as usually assumed, and they are more frequently obtained from freshwater sediments (of arid areas) than from marine sediments.

Schäfer (1972) dealt with the causes of death of birds, and described several examples of bird mass mortalities around the North Sea which were the result of severe weather conditions. Individual dead birds are more common and their death is usually due to accident, disease or old age (although Shipman (1981) stated that death by old age is probably rare in wild animal populations since aged individuals are likely to die of disease, predation or accident rather than senility *per se*).

Schäfer (1972) noted that birds do not sink immediately to the sea bed; the air in the quills, between the feathers, and in the hollow bones keep the carcass floating. He also presented (Schäfer, 1972, p. 46) a disarticulation sequence for herring gulls (*Larus argentatus*), which is summarised below.

The carcass drifts initially on the sea surface, but becomes immersed once the feathers are thoroughly wet. The sequence of break-up and decay is as follows:

1. After 4 days. Young maggots abound in those parts of the carcass that jut out of the water. Although the tissues are soaked with salt water, the maggots thrive and grow rapidly.
2. After 13 days. All skeletal parts above the water surface are now bare of musculature and fibrous tissue. The large flight-feathers which spring from the periosteum of the wing bones have fallen out of their sockets and are lying loosely on the carcass or drift individually away from it.
3. After 27 days. The carcass is still afloat. The head hangs into the water and is well preserved, even skin and feathers. The legs, however, have dropped away; the sternum, too, has separated from the skeleton and has sunk to the sea floor.
4. After 38 days. The body sinks to the sea floor.
5. After 65 days. The carcass, which is still held together by muscles and ligaments, lies on the sea floor. No part of the body floats up again.

Schäfer also noted that if the carcass remains in water the current and tide action will contribute to its disintegration. The following sequence is derived from Schäfer's (1972) notes:

> ..... the hind limbs ..... separate from the trunk, the pelvis from the lumbar vertebrae, and are transported away. Wings, coracoid, clavicle, and sternum continue to hold together as a unit for a long time. The individual parts are frequently twisted longitudinally relative to each other. The head, with the cervical vertebrae, separates from the body, and the tough trachea is left as the only connection between head and body. The skull breaks first between nasal and frontal bones so that the upper part of the break is lost, and the lower part separates later from the joint. The strong flight feathers and tail feathers remain connected with the skeleton for a long time because they are firmly anchored in the periosteum. The down, which is rooted only in the skin, becomes detached when the skin is destroyed.

Schäfer (1972) also described the mummification of birds on the sea-shore and their sub-aerial fossilisation. He described the muscle contractions caused by desiccation, and also observed that the underside of the carcass is moist, continues to decay, and is scavenged by insect larvae and amphipods.

1d3 Taphonomic Faunal Biases

Rich and van Tets (1982) reviewed the fossil avifaunas of Australia and, as a part of their study, they documented the composition and bias of the Australian Neogene avifaunas. They noted that most of the Neogene avian assemblages known on a world-wide scale consist primarily of wetland birds. In this context only such groups as mihirungs (Dromornithidae), emus (Dromaiinae), birds of prey (Falconiformes), pigeons (Columbidae) and owlet-nightjars (Aegothelidae) are not strictly tied to lacustrine or fluviatile environments. Ducks and their kin certainly are, and are by far the most diverse group in the preserved assemblages. Rich and van Tets (1982) regarded this as most likely a preservation bias, as most of the productive sediments are those deposited in lakes and streams, a factor that increases the representation of birds that live in those environments. They qualified this observation by noting that most Australian Neogene fossil bird sites are fluviatile, a few are lacustrine and even fewer are marine. Interpretations of the Neogene avifaunas of Australia must be tempered by the knowledge that each of the assemblages is highly biased in the following ways: 1) few specimens are complete; 2) often certain skeletal elements are abundant while others are lacking or rare; 3) most bird fossils are of medium size, and very few are small (Rich and van Tets, 1982). Wolff (1973, 1975) noticed the same biasing of mammal remains in fluviatile sediments.

Rich and van Tets (1982) postulated that the action of the fluviatile environment on the avian bones prior to burial presumably causes many of the above biases. Thus in any interpretation of fossil avifaunas such biasing should be borne in mind. Their ideas have been presented in a qualitative form only, however, and it is important to quantify their theories with data that can be analysed statistically.

1d4 Experimental Taphonomy

Napawongse (1981) performed experiments on the biostratinomy of bird bones in the fluviatile environment. This work was presented by Rich (1991) within a wider study of the Australasian fossil avifauna.

Napawongse (1981) used two species of birds, *Pachyptila belcheri* (Prion bird), and *Coturnix coturnix japonica* (Japanese Quail). The bones of these species were subject to abrasion and transport experiments.

The abrasion experiments consisted of tumbling the bones in a moderately sorted gravel (mean grainsize -3.18 phi). The bones were tumbled for 150 hours per experimental run. At the end of each experimental run the percentage of original material remaining was calculated. The results are presented in Figures 1.1 and 1.2.

From Figure 1.1 it is evident that the skull, sternum, vertebrae, synsacrum and ribs are abraded and destroyed faster than the pectoral girdle (coracoids, scapulas and furcula), wings (humeri, radii, ulnas, carpometacarpi and digits) and hind limbs (femurs, tibiotarsi, tarsometatarsi and digits). This relates well to what is seen in fossil material (Chapter 6). Figure 1.2 shows the length of time during which individual elements remain recognisable, after abrasion. This indicates that hind limb elements (such as the tibiotarsus and tarsometatarsus) remain recognisable for up to 100 hours of abrasion (Figure 1.3), and this (in conjunction with their diagnostic morphology) may explain why many fossil species have been described on the basis of these elements (pers. obs.).

The transport experiments concentrated on the use of a flume tank. Napawongse (1981) assessed the effect of velocity (and water depth) on different skeletal elements (Figures 1.4 and 1.5). From these results it is evident that bones that have an essentially a cylindrical shape are transported at low velocities by rolling. This increases their susceptibility to transport damage over long periods of time because the skeletal elements are in contact with the substrate for extended periods. Non-cylindrical elements such as the synsacrum and sternum require higher velocities to be transported by rolling but they are transported at low velocities by saltation which quickly damages the bones and produces a rounded "bone pebble"

after short periods of time. This explains why these elements are damaged first in the abrasion experiments.

Napawongse (1981) interpreted the data from these results and compared the results with Voorhies (1969) dispersal groups (Table 1.3). Voorhies dispersal groups are three distinct categories of skeletal elements grouped on the basis of their similar potential for hydraulic transport. Voorhies identified these groups by performing flume experiments on the disarticulated bones of sheep (*Ovis aries*) and coyotes (*Canis latrans*). Although these groups were identified using the bones of mammals, by reproducing these experiments (as Napawongse has done), avian skeletal elements can also be placed into the categories.

In the light of Napawongse's (1981) data (Figure 1.4) I find some of these placements unusual. The furcula, for example, is not transported by rolling and only undergoes intermittent/finite movement even at high velocities, which places it within Group III of Voorhies (1969) as oposed to Napawongse's (1981) placement in intermediate Group II/III. According to Napawongse's (1981) data the skull moves by rolling at moderate velocities which places it within Group II of Voorhies (1969), not within Group III. It is therefore important to re-interpret the dispersal groups of Napawongse (1981). My interpretation of these data is presented in Table 1.4.

The palaeontological importance of this research is that some bones are more likely to be moved by fluvial processes than others. Wolff (1973) referred to these processes and results as "sorting" to denote that the disarticulated bones of a skeleton would be sorted by hydrodynamic processes into groups of readily moved and not readily moved skeletal elements. Behrensmeyer (1975) subsequently elaborated on Voorhies' (1969) scheme, noting that the structural density of bones as well as size and shape influences the probability that a particular bone will be transported. Behrensmeyer discussed the "dispersal potential" of bones in a fluvial medium and noted that:

> ..... since Voorhies Group I is the most easily affected by fluvial transport, its presence or absence in fossil assemblages can provide specific information on the sedimentary history of bone assemblages. (Behrensmeyer, 1975, p. 489).

The absence of Group I bones suggests that the studied assemblage is a lag assemblage (Group I bones having been winnowed out); the presence of Group I bones suggests a non-fluvially winnowed assemblage. Also, presuming that the fluvial transport began at the site of animal death, then:

..... the proportions of different Voorhies Groups in fossil assemblages should provide evidence for the proximity of fossils to the original thanatocoenose and the habitats of the living animals. (Behrensmeyer, 1975, p. 490-491, and Figure 5, p. 491).

The revised interpretation (Table 1.4) of Napawongse's (1981) data is therefore of vital importance for any taphonomic/palaeoecological study of water transported, disarticulated, avian skeletal elements.

Bickart (1984) considered the decay and disarticulation of birds. He charted the decay and disarticulation of the rock dove (*Columba livia*), ring billed gull (*Larus delawarensis*), and herring gull (*Larus argentatus*). The rock doves were freshly killed for the experiment, but the gulls were collected dead, from the shores of a lake, six months previously. Bickart noted that the gulls were frozen shortly after death and that a few had decayed partially. Unfortunately, Bickart did not note whether it was he or the winter environment that froze the carcasses shortly after death, nor did he record how the carcasses were kept.

Twenty-eight carcasses were placed outside on a stream floodplain for one year. Six of the carcasses were placed in cages to protect them against scavengers. The cages were open at the bottom so that the carcasses could rest upon the ground. The climatic conditions and vegetation cover in the area of study were recorded, as well as information on the condition of the stream. The stream flooded regularly to cover the flood plain to a maximum water depth of 30 cm. Little sediment was deposited in these flooding episodes, at most a thickness of 1 to 2 mm.

All but one of the unprotected carcasses were removed either totally or partially from the site by the action of scavengers or by stream action. A trailing device was designed to overcome this, a thread tied to the left tarsometatarsus. Generally this gave the direction of transport, so that bones could be tracked and recovered for further analysis. It was noted that the action of the scavengers was to remove the carcasses from a sedimentary environment with a high probability of burial to one with a low probability.

One unexpected finding of Bickart's (1984) study was that all the specimens that were not removed by scavengers adhered to the ground. This phenomenon happened irrespective of the substrate and was probably due to the action of bodily fluids combined with the ground moisture. Even the most severe storm of the year only managed to move some of the bones in three carcasses (out of a total of seven) that adhered to the substrate. Movement of the carcasses neglected by scavengers were treated in a pictorial/graphical

form by drawing accurately the shape and position of the bones onto a grid on two perpendicular axes (measured in centimetres).

Disarticulation time ranged from 13 days to six months. Table 1.5 shows the disarticulation sequence recorded by Bickart (1984). Bickart (1984) managed to recover some of the bones that had been removed from the site by scavengers and thereby assess the damage that they sustained. Generally the bones were in a fractured and broken state caused by the biting and gnawing action of carnivores. Green-stick fractures (helical, spiral fractures, classification JJJJ, of Davis (1985)) were typical. Bickart's findings are consistent with observation of carnivore damage to mammal bones (e.g. Haynes, 1980; Hill, 1979, 1980; Gifford, 1981; Shipman, 1981).

The weathering of the bird bones over the twelve months of study was slight: it would have corresponded to Stage 0 in Behrensmeyer's (1978) classification of weathering damage for mammal bones (i.e. the bone surface shows no sign of cracking or flaking due to weathering, the bone is usually still greasy, marrow cavities contain tissue and skin, and muscle/ligaments may cover part or all of the bone surface). It can be seen that weathering in a temperate climate is not a significant factor in the breakage and destruction of bird bones as they are more likely to have been destroyed or damaged by scavengers before weathering can have any effect. In a more extreme climate (e.g. a large daily diurnal temperature range), however, the weathering process might have a greater effect.

Although this first attempt to describe experimentally the decay of bird skeletons was very crude in its design and operation, it provides an important foundation on which further outdoor experiments can be built, as well as providing an experimental design which can be modified for further controlled laboratory decay experiments.

Oliver and Graham (1994) described in detail the decay and disarticulation of more than 300 coot (*Fulica americana*) carcasses that were catastrophically killed by freezing into the surface ice of Spring Lake (Tazewell County, Illinois). They charted taphonomic observations for a period of eight weeks. The ice was stable enough to allow terrestrial taphonomic processes to occur. Oliver and Graham (1994) implied that this could create the 'imprintation' of a terrestrial taphonomic signature upon lacustrine deposits.

They recorded the effects of avian and mammalian scavengers upon these carcasses and identified different modes of attack. Avian scavengers preferentially fed on the head, neck, and breast-wing complex, whereas mammalian scavengers fed on the hindlimb and tail regions. These

scavengers created distinct disarticulation pathways and distinctive bone breakage patterns. After carcasses are no longer attractive to scavengers, anatomy becomes the most important factor in disarticulation patterns (Oliver and Graham, 1994).

Oliver and Graham (1994) identified the following disarticulation sequence (by summation of the joint frequencies (the number of surviving individual joints) of 27 scavenged carcasses):

1. The cervical-skull unit disarticulated from the thoracic vertebrae.
2. The skull separated from the cervical vertebrae, and simultaneously the sternum and associated wing complex dropped from the trunk.
3. The sternum-coracoid was severed.
4. The femur-synsacrum joint was severed and the hindlimb dropped from the trunk.
5. The thoracic vertebrae disarticulated from the synsacrum.
6. The coracoid dropped from the humerus and simultaneously the tarsometatarsus-phalanges unit disarticulated from the upper hindlimb.
7. The phalanges disarticulated from the tarsometarsus.
8. The tibiotarsus and femur disarticulated.
9. The humerus disarticulated from the lower wing unit.
10. The radius-ulna disarticulated from the carpometacarpus and phalanges.

Oliver and Graham (1994) noted that this summary disarticulation sequence based on final observations of carcass condition emulates time-averaging in the fossil record, but may obscure disarticulation patterns that occurred earlier. In other words , the last frame of a film may accurately document the end result, but it may not clearly reflect all of the processes recorded in the previous frames.

Oliver and Graham (1994) then produced further disarticulation patterns (by separating the bird and mammal scavenged carcass data) for comparison between avian and mammalian scavenged carcasses.

<u>Bird-scavenged</u>

1. Skull-cervical unit dropped from vertebral column.
2. Sull disarticulated from atlas.
3. Sternum-coracoid-wing unit became disassociated from trunk.
4. Sternum disarticulated from coracoid-wing unit.
5. Thoracic unit dropped from synsacrum-hindlimb unit.
6. Coracoid disarticulated from humerus.

7. Hindlimbs dropped from synsacrum as femur-synsacrum joint was severed.
8. Wings became disassociated.
9. Femur and tibiotarsus disarticulated.

Mammal scavenged

1. Tarsometarsus-phalange unit disarticulated from tibiotarsus.
2. Simultaneously, (a) phalange unit disarticulated from tarsometatarsus, (b) skull-cervical unit dropped from vertebral column and (c) skull dropped from cervical unit.
3. Simultaneously, (a) femur-tibiotarsus unit dropped from synsacrum, and (b) femur and tibiotarsus disarticulated.
4. Simultaneously, (a) thoracic unit disarticulated from synsacrum, (b) sternum and coracoid disarticulated, and (c) at least one wing unit disarticulated from sternum-coracoid complex.
5. Coracoid disarticulated from humerus.

Oliver and Graham (1994) compared these sequences with that of Schäfer (1972) (see above for summary of Schäfer, 1972). They revealed a pattern broadly similar between Schäfer's (1972) sequence and their sequence noted for mammal scavenged coot carcasses. Oliver and Graham (1994) suggested that mammalian scavenging may have played a role in the sequences that Schäfer (1972) noted for bird carcasses observed in and around the North Sea.

Oliver and Graham's (1994) comparison of their disarticulation sequences with those of Bickart (1984) (see above for summary of Bickart, 1984) revealed several differences. Oliver and Graham (1994) suggested that the joint frequency table of Bickart (1984) indicated that microhabitat conditions played a critical role. They also suggested that the mesh size (used by Bickart, 1984) of the protected specimens was not small enough to prevent scavenging by rodents and that this may explain the early loss of some of the hindlimb joints (Oliver and Graham, 1994). They further indicated that the differences in disarticulation could be, in part, due to climatic differences and decay/disarticulation processes caused by 'natural decay' and microscavengers (e.g. maggots, fungi, worms) as opposed to larger scavengers where the attack is largely mechanical in nature (Oliver and Graham, 1994).

1e Summary and Aims

A number of papers have contributed to the development of ideas on avian taphonomy. These are considered above, and are summarised in Table 1.6.

From these papers it is possible to identify a series of the most important questions that have yet to be answered, and which this thesis attempts to address in the following chapters.

1. How do different bird skeletons disarticulate?
2. In what order does this disarticulation take place?
3. How long does the disarticulation process take?
4. What conditions affect the process?
5. How do experimental data compare with data collected from modern environments?
6. What, if any, special fossilisation processes are operating in the preservation of feathers?
7. Which feathers are most readily fossilised?
8. Which feathers are the most resistant to decay?
9. Why are isolated feathers found in sediments that do not contain bones?
10. How do differing environments preserve avian remains?
11. In which environments does taphonomic biasing occur?
12. What implications for other flying vertebrates can be drawn from a study of fossil birds?

Age	Formation	Locality	Environment	Notes	References
Maas-trichtian	Lecho	Salta Province, Argentina	Terrestrial	Many fragmentary remains of terrestrial? enantiornithine birds.	Walker,1981; Chiappe, 1993.
Maas-trichtian	Hornerstown, Navesink	New Jersey, USA	Marine	Approximately 20 specimens of broken, isolated bones. The fauna is comprised of aquatic and one possible marine species.	Olson and Parris, 1987.
Santonian - Campanian	Barun Goyot	Gobi Desert, Mongolia	Terrestrial	Two complete, 2 skulls and 5 fragmentary embryos of *Gobipteryx minuta*. The fauna only contains these terrestrial? enantiornithines.	Elzanowski, 1974; 1977; 1981.
Coniacian	Rio Colorado	Nuquén Province, Argentina	Marine	Two partially complete individuals and other fragmentary bones of *Patagopteryx*, a cursorial bird.	Bonaparte 1991.
Coniacian - Campanian	Niobrara, Pierre Shale, Foremost	Central States of USA and southern Canada	Marine	Many specimens of birds. Specimens range from complete and articulated to isolated, broken bones. The fauna is totally comprised of marine genera e.g. *Hesperornis*, *Ichthyornis*, *Baptornis* and *Parahesperornis*.	Bennett, 1990.
Albian	Cambridge Greensand	Cambridge, UK	Marine	Many isolated, fragmentary remains of the marine genus *Enaliornis*. The bones are generally abraded and rounded.	Elzanowski and Galton, 1991.
Barremian - Aptian	Unduruhinskaya	Bajan-Khongor aimak, Mongolia	Lacustrine	Specimens of partially articulated ambiortids: *Ambiortus dementjevi* and *Holbotia ponomarenkoi*. This locality also preserves feathers.	Kurochkin, 1985.
Barremian	"Calizas de La Huérgina	Las Hoyas, Cuenca, Spain	Coastal flats / Lacustrine	Almost fully articulated post-cranial skeletons of *Iberomesornis romerali* and *Concornis lacustris*. The locality also preserves feathers.	Sanz and Bonaparte, 1992; Sanz *et al.*, *in press*.

Table 1.1 Important Mesozoic fossil bird localities.

Age	Formation	Locality	Environment	Notes	References
Valanginian	Jiufuotang	Liaoning Province, China	Lacustrine	Possibly the most imortant Mesozoic site for avian remains. Abundant partially complete skeletons. So far only two arboreal birds, *Cathayornis* and *Sinornis* have been described but there are at least 15 other specimens.	Sereno and Rao, 1992; Zhou *et al.*, 1992; and D. Unwin *pers. comm.*
Tithonian	Solnhofen Limestone	Altmühl-Alb, Bavaria, Germany	Restricted Marine Lagoon	Seven skeletal specimens with feather traces and one feather of *Archaeopteryx* spp. All specimens are well preserved and either complete or partially complete.	Wellnhofer, 1993.

Table 1.1 (cont.) **Important Mesozoic fossil bird localities.**

Age	Formation	Locality	Environment	Notes	References
Pleistocene	Palos Verde Sand	Rancho La Brea, Los Angeles, USA.	Terrestrial Tar Pit 'Trap'	1000's of well preserved, isolated bones. 67% of bones are those of birds of prey. Further details in Chapter 6.	Howard, 1962a; 1962b; Stock, 1956
Pliocene	Varswater	Langebaanweg South Africa	Marine to Terrestrial.	100's of well preserved bones. The fauna (terrestrial, aquatic and marine birds) is mixed as the formation represents a marine transgression.	Rich, 1980; Olson 1985b
Pliocene	Lee Creek	N. Carolina, USA.	Marine	1000's of isolated well preserved bones from a phosphorite deposit. Fauna is marine dominated.	Olson 1985
Miocene to Pleistocene	Various	Florida, USA.	Marine to Terrestrial.	10000's of isolated bird remains. The fauna is mixed as the deposits represent calcareous beach and marine deposits	Hulbert Jr., 1992; Emslie and Morgan, 1994.
Miocene	San Mateo	Oceanside, California, USA.	Marine	100's of isolated bones. The fauna represents a 'normal' North Pacific avifauna.	Howard, 1982
Miocene	Calcareous sediments infilling impact crater	Nördlinger Ries, Germany	Lacustrine	100's of isolated, well preserved bones. The faunais dominated by aquatic birds but it also contains large numbers of terrestrial birds eg. Passerines	Ballmann, 1983
Miocene	Calvert	Maryland, USA	Marine	100's of isolated,well preserved birds. The fauna is dominated by marine birds especially pseuodontorns. An important site for Miocene marine birds.	Wetmore, 1938; 1941; Olson, 1985.
Miocene	??	St. Gerand Le Puy, France	Lacustrine	Over 30,000 bones have been recovered. The avifauna is comprised of marine and aquatic species	Cheneval, 1989
Eocene - Oligocene	??	Quercy, France	Lacustrine infilling karstic topography	1000's of isolated well preserved bones. The fauna is mixed with aquatic species dominating.	Mourer-Chauviré, 1982.
U. Eocene - L. Oligocene	Florrisant	Colorado, USA	Lacustrine	Small numbers of exceptionally well preserved birds (including those preserved with feathers). Fauna is dominated by wading birds and other aquatic species.	Allen, 1878; Shufeldt, 1917.

Table 1.2 Important Cenozoic fossil bird localities.

Age	Formation	Locality	Environment	Notes	References
Eocene	La Meseta	Seymour Island, Antarctica	Marine	100's of isolated bones. The fauna almost completely consists of penguin remains. The most important early tertiary deposit in the southern hemisphere. Further details in Chapter 6.	Simpson, 1971
Eocene	London Clay	S.E. England	Marine	100's of isolated well preserved bones. Also occassional well preserved articulated specimens. The fauna is mixed and is derived from an inland Eocene Tropical rain forest.	Harrison and Walker, 1977
Eocene	Green River	Colorado and Wyoming, USA	Lacustrine	Approx. 50 well preserved and partially disarticulated specimens. The fauna is dominated by waterbirds and other birds that live in the surrounding ecotome. Further details in Chapter 6.	Grande, 1984.
Eocene	Oil shales	Messel, Germany	Lacustrine	100's of well preserved specimens (including soft tissues). The fauna is dominated by wading birds although it does contain other terrestrial and aquatic birds. Further details in Chapter 6.	Peters, 1992.
Eocene	Lignites	Geisaltal, Germany	Lacustrine / Swamp	100's of well preserved specimens (including soft tissues). The fauna is dominated by wading birds although it does contain other terrestrial and aquatic birds.	Lambrecht, 1933.
Palaeocene	'Moler' (Fur) Formation	NW Jutland, Denmark	Restricted Marine	Over twenty remains of birds (mainly incomplete skeletons) have been found. The assemblage is unusual in that all the finds are of a typical 'land assemblage'.	Hoch *et al.*, 1983; Bonde, 1987.

Table 1.2 (cont.) **Important Cenozoic fossil bird localities.**

GROUP I. Immediately removed, transported by saltation or flotation.
Ribs, vertebrae.

INTERMEDIATE GROUP I/II.
Phalanx.

GROUP II. Removed gradually, transported by traction.
Pelvis, sternum, mandible, coracoid, scapula, humerus, ulna, radius, carpometacarpus, femur, tibiotarsus, tarsometatarsus.

INTERMEDIATE GROUP II/III.
Furcula.

GROUP III. Lag deposits.
Skull.

TABLE 1.3 **Voorhies grouping of avian skeletal dispersal groups, (from Napawongse, 1981).**

GROUP I. Immediately removed, transported by saltation or floatation.
Phalanax, ribs, vertebrae.

INTERMEDIATE GROUP I/II.
Carpometacarpus.

GROUP II. Removed gradually, transported by traction.
Skull, mandible, scapula, ulna, radius, femur, tibiotarsus, tarsometatarsus.

INTERMEDIATE GROUP II/III.
Coracoid.

GROUP III. Lag deposits.
Pelvis, sternum, furcula, humerus.

TABLE 1.4 **Reinterpretation of Voorhies grouping of avian skeletal dispersal groups (after Napawongse, 1981).**

Order of Disarticulation	Joints Disarticulating
1	Sternum-ribs; Coracoid and scapula-humerus
2	Synsacrum-ilia and ischia; Sternum-coracoid; Pelvis-femur; Femur-tibiotarsus; Tibiotarsus-tarsometatarsus; Tarsometatarsus-phalanges
3	Skull-lower mandible; Skull-atlas; Cervical vertebrae-cervical vertebrae; Cervical vertebrae-thoracic vertebrae; Thoracic vertebrae-pelvis; Pelvis-caudal vertebrae; Thoracic vertebrae-ribs; Humerus-radius and ulna
4	Coracoid - scapula; Radius proximal-ulna proximal; Radius distal-ulna distal; Radius and ulna-carpometacarpus; Carpometacarpus -digit 2; Digit 2, phalanx 1-digit 2, phalanx 2

TABLE 1.5 **Joint disarticulation for rock doves and ring billed gulls in a stream floodplain environment (after Bickart, 1984).**

Author/s	Date	Content
Schäfer	1962/1972	First anecdotal decay observations
Napawongse	1981	First avian biostratinomy experiments
Rich and van Tets	1982	First avifaunal analysis incorporating taphonomic considerations
Bickart	1984	First avian disarticulation experiments
Oliver and Graham	1994	Detailed observational taphonomy and disarticulation experiments

TABLE 1.6 Summary of papers in avian taphonomy.

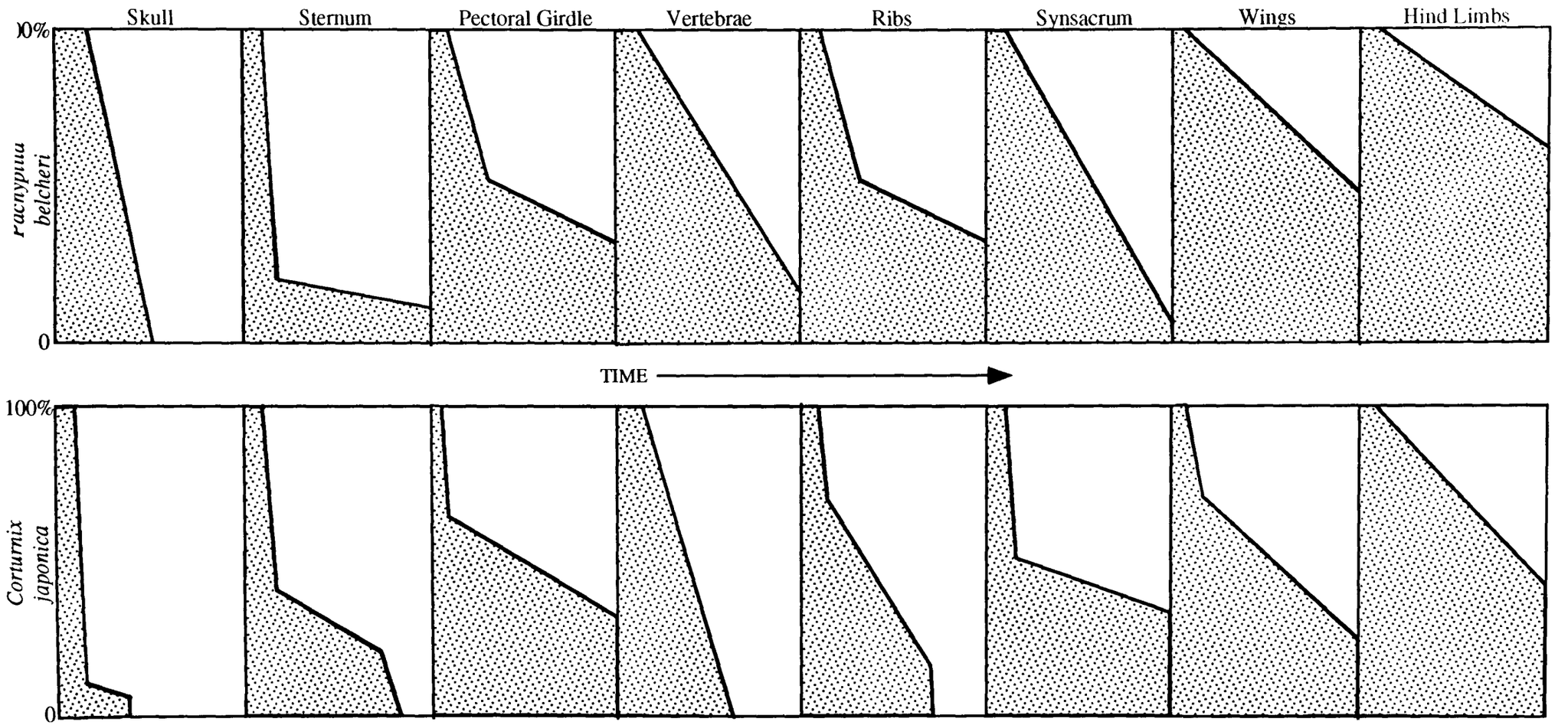


FIGURE 1.1 **Graphs showing how bones differentially wear in a fluviatile environment. *Pachyptila belcheri*, which has densely ossified bone, is compared with *Coturnix japonica* which is less densely ossified. Percentage of original material remaining was calculated at the end of 10 experimental runs (approx. 150 hr./run, for a total of 1650 hours) (y axis), after Napawongse (1981).**

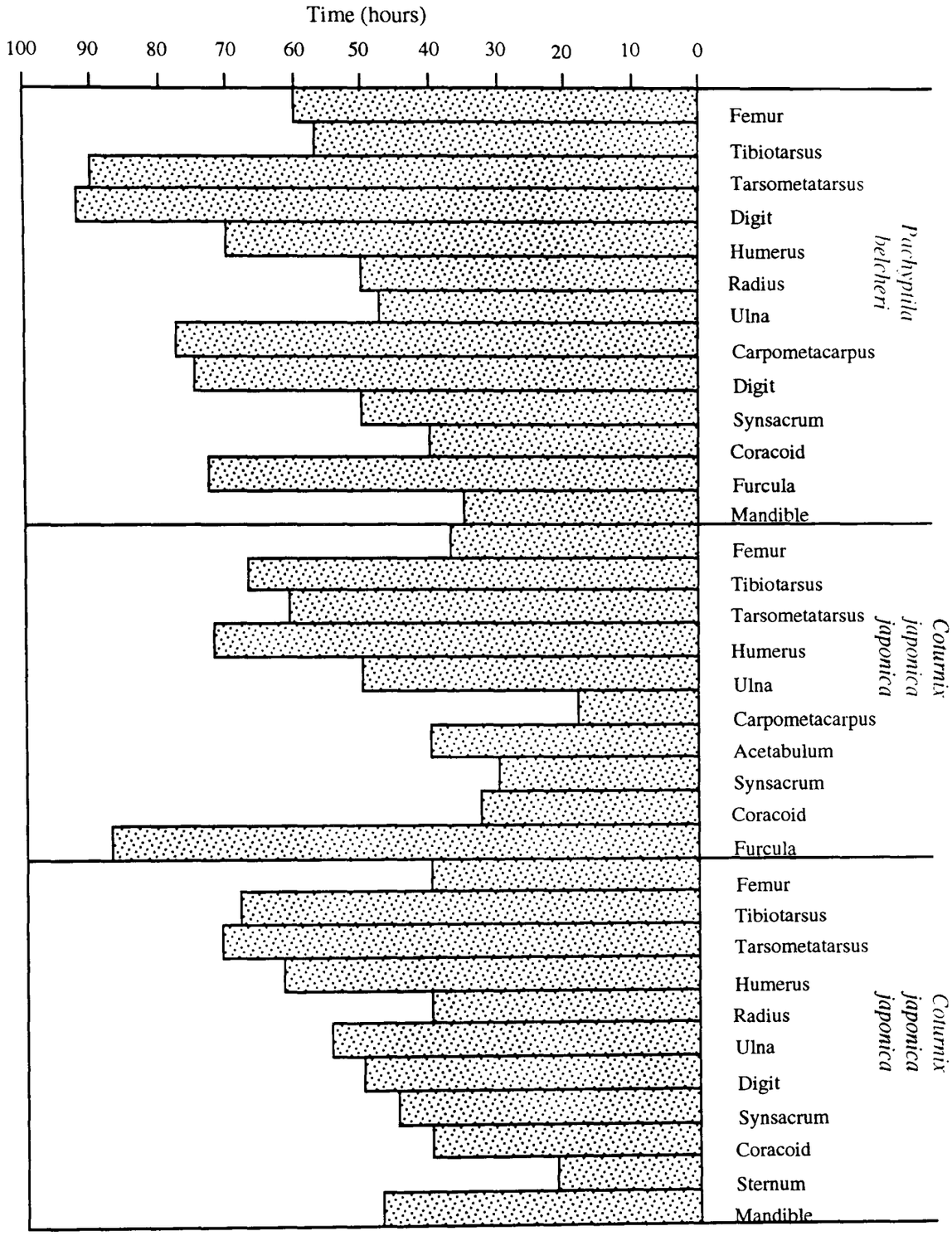


FIGURE 1.2 **Erosional effect of simulated fluviatile environment on two species of birds, a seabird (*Pachyptila belcheri*) and two specimens of a terrestrial bird (*Coturnix japonica*). The horizontal scale represents thenumber of hours during which bones were tumbled in water and a moderately sorted gravel (-3.18 phi). Bones could be recognised for the period indicated by the stippled columns (after Napawongse, 1981).**

FIGURE 1.3 Generalised avian skeleton showing the bones (in black) that are most resistant to abrasion. (After Napawongse, 1981).

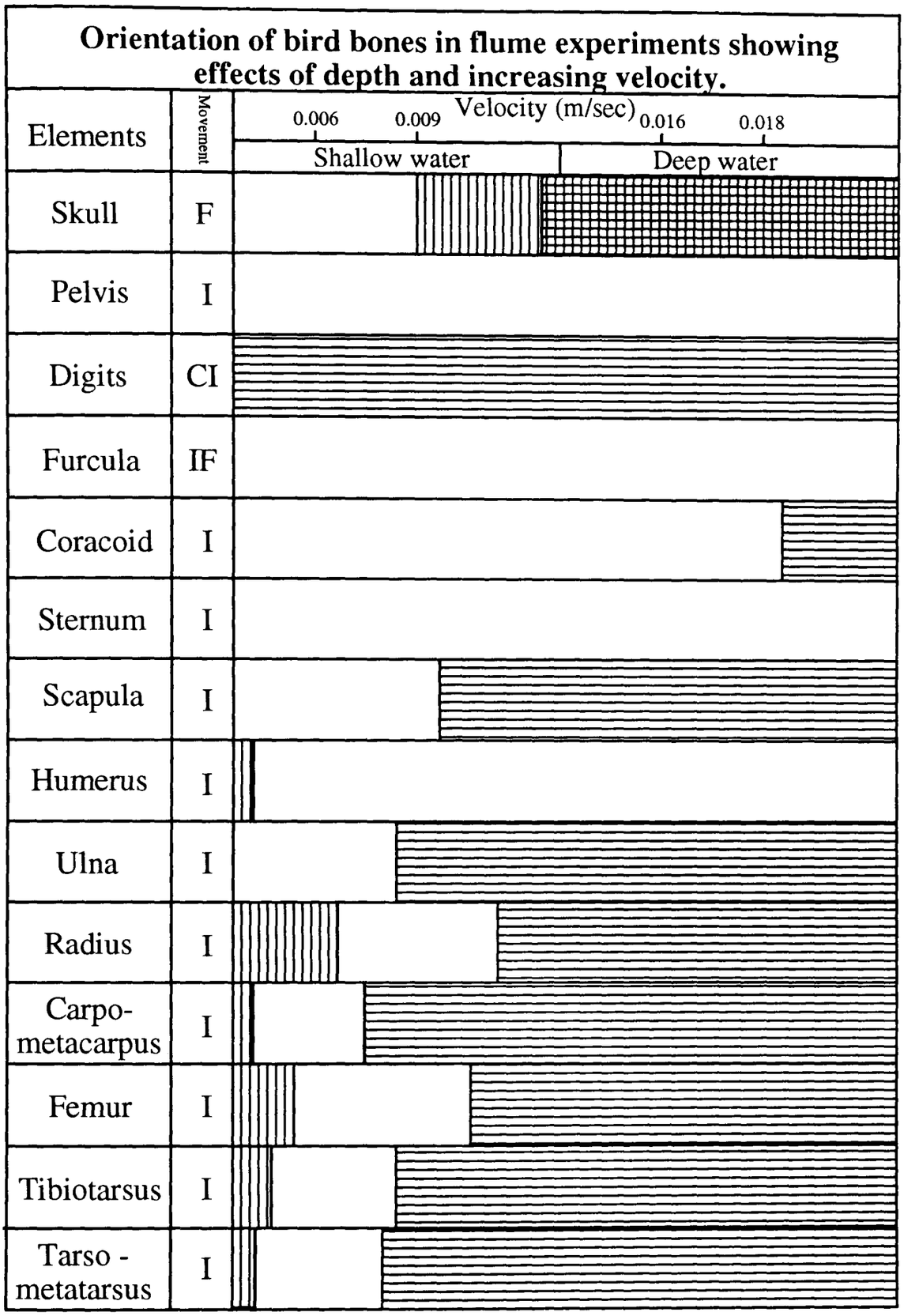


FIGURE 1.4
Effects of speed and depth on the orientation and transport of bird bones (after Napawongse, 1981).

LEGEND

Orientation

- Transverse
- Parallel

Movements

- Rolling
- C Continuous
- I Intermittent
- F Finite

	Shallow water orientation		Deep water orientation		Polarity (Parallel to currer	
Elements	Parallel	Transverse	Parallel	Transverse	Large end downstream	Small enc downstrea
Femur	11	1	6	2	6	11
Tibiotarsus	9	2	12	0	8	17
Tarso-metatarsus	11	0	13	0	1	23
Humerus	12	1	14	0	4	22
Radius	11	1	12	0	9	14

FIGURE 1.5 Orientation of bird long limb bones in flume experiments showing effects of depth of water. After Napawongse (1981).

Chapter Two
The Decay, Decomposition and Disarticulation of Birds

2a. Introduction

The decay of birds can be investigated in two ways, either by actualistic experiments or by field observations. Bickart (1984) carried out actualistic experiments in a terrestrial environment. This approach was of limited value because terrestrial accumulations of avian remains are rare in the fossil record (although it does indicate why fossil birds are rare from these environments). Therefore a more realistic preservation environment was adopted for my experiments. Schäfer (1972) used field observations to produce a "timing of disarticulation" for gulls, but he did not describe how degradation proceeded. Chapter 4 describes how data produced in these actualistic experiments can be used to interpret fully data obtained from observation of taphonomic processes in the field.

2b. Actualistic Decay Experiments

2b1. Experimental method

To investigate the decay of bird cadavers it was essential to carry out the experiments within an environment where decay would be rapid enough to observe on a daily basis. Therefore the sub-tropical environment of the Everglades, Florida was chosen.

Two field sites (Figure 2.1) were selected from several surveyed in southern Florida. Site selection was based the following criteria: availability and ease of access, one site must be freshwater and one sea water, the ability to complete the experiments i.e. away from disturbance by people, water not too deep or shallow. Site one is a freshwater environment (16-23 ppt salinity) in which biogenic carbonate muds are forming. The muds are only deposited (by flocculation) when the water pH reaches a value of 9 (pers. comm. Dr. Earl Rich). The sediment is organic rich from plant matter (predominantly Sawgrass (*Cladium jamaicensis*)). The surface of the sediment is covered by a mat comprised of green algae and diatoms. Below the mat (depth approximately 5cm) the sediment turns from a beige to a grey/black colour. This horizon smells slightly of hydrogen sulphide showing that the sediment at this depth is within the zone of sulphate reduction (see Allison and Briggs, 1991).

Site two is a marine environment (30-34 ppt salinity) in which organic rich muds are being deposited. The sediment is rich in organic matter from the surrounding mangrove vegetation (red mangrove - *Rhizophora mangle*). It becomes anoxic within one centimetre of the sediment-water interface due to the decomposition of this organic matter. It smells strongly of hydrogen sulphide and is black in colour, below the brown surface layer. The sediment was observed to contain iron monosulphides which account for the black colour and also explain the brown surface colour of the sediment ($FeS + O_2 \Rightarrow Fe_2O_3$ + soluble sulphates). The presence of the monosulphide complexes also indicates that the horizon of sulphate reduction is very close to the sediment surface. The depth of sediment (to the bedrock of Quaternary limestone reef complexes) was twenty to thirty centimetres and the presence of large quantities of gastropod and bivalve shells at the base indicates that the sediment was in equilibrium with regard to carbonate (CO_3^{2-}).

The environmental conditions of the site (air and water temperature, humidity, rainfall, wind speed, current speed and direction, salinity, dissolved oxygen content, pH and water depth) were recorded daily over the seventy day period of the experiment (Table 2.1).

Sixty-four specimens of birds (23 genera, 27 species, see Table 2.2) were used. They were obtained from a wildlife rehabilitation centre where they had died of natural causes. Immediately upon death the carcasses were placed in a freezer. Before being used in the experiments they were defrosted and accurately weighed.

Specimens were separated into two size categories, large and small, based on wing span (greater and less than 0.65 metres respectively). Experiments with large and small carcasses, both protected and unprotected, were set up in both field sites (eight categories of experiment in total) (Table 2.3).

Protected specimens were placed in specially constructed wire cages. The dimensions of the small cages were:- length 264mm, width 105mm, height 55mm; and those of the large cages:- length 400mm, width 400mm, height 500mm. The cages were constructed of 2mm zinc galvanised wire (mesh size $25mm^2$) and then covered with fibreglass 'mosquito netting' (mesh size $1.5mm^2$). The base of the cage was left open to allow the specimens to contact the sediment. To prevent the cages from being moved they were fixed to the sediment with three large (20cm) plastic tent pegs.

Unprotected specimens were anchored to the sediment surface by tying them to large diving belt weights using one metre of 20lb breaking strain nylon monofilament fishing line attached to both tarsometatarsi. This allowed

the specimens to move freely (i.e. to float or sink) and also prevented scavengers from removing the carcass from the experimental area.

Experiments in each of the eight categories were terminated at 1, 4, 7, 11, 28, 56, and 70 days after the start of the experiment. The specimens were collected by passing a large, fine mesh fishing net through the sediment underneath them, minimising disturbance to the arrangement of the cadaver. The bones were placed in a large, heavy duty plastic sack and transferred to a cool box to inhibit any further decay processes. Samples for SEM were carefully removed by dissection with sterile instruments. These samples were transfered to sterile containers and fixed using the hexamethyldisilizane (HMDS) method (Nation, 1983). The specimens were placed in a fume cupboard within a refrigerated room and allowed to dry for one day. They were then carefully removed from the surrounding sediment by slowly peeling dried sediment away from the carcass, and their orientations were noted and photographed. The specimens were then weighed.

For each specimen it was possible to calculate the percentage weight loss by using the following equation.

$$[2.1] \qquad \%WL = 100 - (W/Wo \times 100)$$

where: %WL = percentage weight loss; W = weight after decay; Wo = weight before decay.

Percentage weight loss was used in order to take account of weight variation within the sample of birds used. To show these results graphically percentage weight loss was plotted against time for the eight sample categories (Figures 2.2 to 2.16) (see Appendix 4 for data). The gradient of the curve equates to decay rate because the variables plotted are weight loss against time (see Chapter 2b6. for an account of the statistical methods used).

2b2. Evidence of Scavenging

The processes of scavenger attack on carcasses were observed in the unprotected samples. The scavengers were divided into large and small scale, which coincides with vertebrate and invertebrate scavengers.

Large scale scavengers:- The large scale scavengers were all vertebrates. In the freshwater locality these were raccoons (*Procyon lotor*), alligators (*Alligator mississippiensis*), and fishes. In the salt-water the scavengers were alligators, crocodiles (*Crocodilus americanus*), turkey vultures (*Cathartes aura*) and fishes.

Each scavenger had a distinct trait. Alligators and crocodiles attacked the cadavers, tearing them from their securing lines, and either eating the body whole or transporting it to a "store" and burying it under the sediment until required (pers. obs.). A "store" discovered thirty metres away from the freshwater experiment site contained the remains of two cadavers. The "store" was a shallow depression approximately ten centimetres deep, presumably excavated by the alligator. The cadavers had been placed into this store and covered with sediment until they were invisible. The alligators and crocodiles removed 31% of specimens in the freshwater (n=32) and 44% of specimens in the salt-water environment (n=32).

Racoons, highly intelligent scavengers, could only reach the field site when water levels were low enough for them to wade or make short swims. They investigated the large protected specimens by up turning the cages after removing the plastic pegs. They never removed or consumed any specimens but their activities resulted in premature disarticulation.

Turkey vultures removed floating, unprotected specimens and then transported them to nearby land where they fed on the flesh. This was followed by scavenging and disarticulation by land based predators including small mammals, land crabs and insects.

Fish removed small amounts of flesh, although in large numbers over a period of time this caused disarticulation.

Small scale scavengers:- The small scale scavengers included several species of crayfish (e.g. *Procambarus gracilis*), giant water scavenging beetles (*Hydrophilus triangularis*) in freshwater and the Crown Conch gastropod (*Melongena corona*) in salt-water.

Crayfish activities were mainly nocturnal, but they also fed under the larger carcasses during the day.

The most efficient and abundant scavenger in salt-water was the Crown Conch. These gastropods were attracted to the carcass in large numbers. Once the cadaver sank sufficiently close to the substrate the Crown Conch colonised it rapidly. At one stage during the experiment over fifty individuals were found attached to one pelican leg (Figure 2.17). This extra mass quickly sank the cadaver completely and rapid, total colonisation occurred. From this point the gastropods took only three days to reduce the pelican carcass to bone and inaccessible joint ligaments. The implications for vertebrate taphonomy of this previously unrecorded gastropod scavenging are as follows:

1. Disarticulation of the skeleton is much quicker than anticipated, especially where carnivorous gastropods are abundant within the benthos;

2. If disarticulation is hastened by gastropod scavenging then elements of the carcass will be separated by transport at an earlier stage.
3. Diet of extinct gastropods is almost impossible to determine, therefore the importance of scavenging is difficult to estimate from the fossil record;

2b3. Autolysis and Bacterial Decay

The soft tissues of the specimens rapidly broke down due to autolysis of the tissues by enzymes from within the body (Figures, 2.18 and 2.19). The efforts of autolysis can be distinguished from bacterial decay by investigating internal structures after death, since external decay agents (e.g. bacteria) would not have had time to colonise these. However, after a short period of time (approximately 2 days) autolytic breakdown is accentuated by the colonisation of tissues by the bacteria.

Bacteria are autochthonous within the living animal especially within the gastric and circulatory/respiratory systems. These bacterial numbers are kept within physiological levels by the immune system in a healthy bird. The immune system "shuts down" on death and colonisation of the cadaver can occur from within, in a few hours (Coles, 1985). Abnormally high starting numbers of bacteria may occur in a bird that died of a bacterial disease such as salmonellosis, avian typhoid, tuberculosis or avian cholera (Coles, 1985). Allochthonous bacteria from the surrounding environment will quickly colonise the carcass in the following ways: 1. keratin-specific bacteria attack the feathers, beak and leg scales (Chapter 5); 2. bacteria enter the body either via a bodily orifice (e.g. mouth, anus/genital region) or through a skin contusion or laceration. Once inside the cadaver the bacteria rapidly colonise surrounding tissues.

Under natural freshwater conditions four types of bacteria were found in the pectoralis muscle of an osprey (*Pandion halietus*) after one day of decay (Figures 2.20 and 2.21). The pectoralis muscle was chosen because it would take the same time for both allochthonous and autochthonous bacteria to reach this portion of the carcass (Coles, 1985). The four types of bacteria identified were: 1. bacilliform ca 4μm in size; 2. bacilliform ca 2μm in size; 3. coccoid ca 1μm in size; and 4. bacilliform (with a hemispherical projection) ca 3μm in size. All four species of bacteria attached themselves to the muscle tissue by a glycocalyx. The majority of bacteria (both gram positive and gram negative) in the natural environment grow in glycocalyx-enclosed microcolonies attached to inert surfaces (Williams *et al.*, 1990). This mode of growth enables the bacteria to occupy and persist in a suitable environment, and their fibrous anionic glycocalyx serves both to trap nutrients and cations by acting as an ion exchange resin, and to protect them from attack by

bacteriophage and phagocytic cells. Glycocalyx is predominantly made of exopolysaccharides which bind to the outer cell wall surface of the bacteria. The glycocalyx is often comprised of a fibrous matrix 0.5-1.0 μm in width and, in specialised cases, bacteria that digest insoluble nutrient substrates such as cellulose are able to attach specifically to their nutritive substrate. These types of bacteria use their enveloping glycocalyx matrix so that surface-bound enzymes can digest the substrate, and to bind and channel the resultant soluble nutrients back to the bacterial surface.

2b4. Morphological Stages of Decay

A decay sequence can be constructed by using visual qualitative methods (see Appendix 7). This decay sequence can be divided into decay stages. These stages were found to be the same in fresh and sea water. The stages are as follows (Figures 2.22 to 2.32):

1. The skeleton remains intact and the feathers are still attached to the dermal layers. The internal soft tissues remain, but are undergoing autolysis and bacterial decay. This stage occurs from one to three days in protected specimens and up to two days in unprotected specimens (Figure 2.22).

2. The skeleton is still complete, but the soft tissues have decayed and loosely attached feathers (down, contour etc.) are starting to become detached (Figure 2.23).

3. The skeleton is now starting to disarticulate. Disarticulation occurs in a set order though some overlap occurs.

3.a. The skull and cervical vertebrae detach from the thorax. The skull may remain attached to some cervical vertebrae but it is more usual for these two elements to be totally separated from each other (Figure 2.24).

3.b. The femur disarticulates from the synsacrum (Figure 2.25).

3.c. The pectoral girdle becomes detached from the thorax. The pectoral girdle and forelimbs (wings, sternum, clavicle, coracoids and scapulae) remain articulated as a unit (Figure 2.26).

3.d. The vertebrae in the abdominal region disarticulate. This causes the thorax to separate from the synsacrum (Figure 2.27).

3.e. The ribs disarticulate from the thoracic vertebrae and the thoracic vertebrae disarticulate into individual vertebrae (Figure 2.28).

3.f. The legs separate into individual elements (femur, tibiotarsus, tarsometatarsus and digits) (Figure 2.29).

3.g. Final disarticulation occurs between elements of the pectoral girdle (the wings, sternum, clavicle, coracoids and scapulae) (Figure 2.30).

Depending on various external, i.e. environmental factors (e.g. current strength, scavenging, decay above or below the sediment) the elements of the disarticulated skeleton may remain juxtaposed in the sediment, or individual bones may be removed from the area, resulting in a skeleton that appears articulated but lacks some bones. Both these configurations are classified as stage 3, because the difference is caused by external effects and is not a true reflection of the decay pattern.

4. The skeleton disarticulates completely and external forces may remove skeletal elements (Figure 2.31).

5. Only isolated, completely disarticulated, skeletal elements remain. These elements may exhibit damage caused by external forces (Figure 2.32).

2b5. Formation of Authigenic Minerals

The sediments in the two field sites were anoxic (Chapter 2b1.), and decomposition of the abundant organic matter led to the formation of iron monosulphides. Iron monosulphides were found to have formed within the bones of some of the experimental specimens. These authigenic minerals occurred within the bones of ovenbirds (*Seirus aurocapillus*, which are small, a weight of approximately 17 grams). The specimens were from the SSP category (sea water, small, protected; see Table 2.3) and had been decaying for 56 to 70 days. It was not possible to identify the iron monosulphides directly because as the bones dried (to be weighed) the unstable monosulphides reverted to stable iron III oxides. This process was identified by the change in colour of the bones from black to rust brown.

The formation of the iron monosulphides only occurred in the SSP specimens (see Table 2.3) that were buried quickly in the marine environment. The reasons for this are threefold:

1. Rapid burial in the marine environment allowed the ovenbirds to decay within the zone of sulphate reduction (no rapid burial occurred in the freshwater environment so, although the sediment was in the zone of sulphate reduction, the specimens did not decay within it).

2. The bones of the ovenbirds were small. Hence, microenvironments were created within the medullary cavity which allowed the formation of monosulphides.

3. The walls of the bones were thin, allowing the easy diffusion of ions (e.g. sulphide and iron ions) through the bone to the medullary cavity. If the walls were thicker diffusion of ions would have been retarded (i.e. diffusion only through bone foramina).

Within the fossil record pyritised bird bones are rare. The only locality that does yield pyritised fossil bird bone is the offshore marine, Eocene, London Clay deposits of the S.E. England (pers. obs., see Allison, 1988). The fossil bird bones that contain pyrite are small (< 9 mm in diameter) (pers. obs.). This apparent rarity of pyritised bird bones requires explanation. Examination of fossil bird bones from the London Clay deposits revealed 10 bones (71%, n = 14) that contained pyrite (see Table 2.4). Measurement of the diameter (two values were obtained, the a and b diameters, as the bones had an elliptical cross section, see Figure 2.33) of bones yielding pyrite (Table 2.4) were recorded. These data revealed that bones with a cross sectional area of less than 38mm^2 were completely filled with amorphous, non-crystalline pyrite (with one exception, one bone with a cross sectional area of 172mm^2 was completely filled with pyrite). Those bones with a cross sectional area of 53mm^2 and above only had a crystalline pyrite coating on the internal medullary cavity (with one exception, see above). Although this data set is small (and consequently statistically invalid) it does indicate that diameter is important in controlling the formation of pyrite within the bone. It is possible (although not totally satisfactory) that the scarcity of pyritised bird bones is due to the lack of input of small bird bones into sedimentological regimes in which pyrite is formed. This lack of small birds inhabiting such sedimentological regimes is discussed further in Chapter 6.

2b6. Weight Loss and Decay Rates

Graphs (percentage weight loss versus time) of the quantitative data (64 specimens) (Figures 2.2.2 to 2.2.16) show an exponential decay. The curves were fitted to the plotted data points using the computer package Kalaeidograph. The significance of the fit was assessed using the Pearson product moment correlation, R. Values for R ranged between 0.83 and 0.90 which indicates a significant correlation. There is little difference between the graphs (Figures 2.10 and 2.11) for protected and unprotected specimens (linear regression test, R = 0.89), except that the unprotected specimens show a slightly more rapid weight loss (denoted by the steeper gradient in the early part of the curve). The unprotected specimens are reduced to between zero and twenty percent of their original weight within three to ten days, whereas the protected specimens require between ten to twenty-eight days to undergo the same weight loss. This is expected because the scavenging that occurs in the unprotected specimens increases the rate of weight loss.

It is also evident that size does not influence rate of weight loss in unprotected specimens (Figures 2.10 and 2.11) (linear regression test, R = 0.95). In protected specimens, on the other hand, where medium and large

scale predators are excluded, smaller specimens show a faster rate of weight loss (Figures 2.12 and 2.13).

There is very little statistical difference between decay rates within the two differing environments (Figures 2.14 and 2.15) (linear regression test, R = 0.95). Both environments have a range of predators and scavengers (Chapter 2b2.), which although different are equally efficient.

As decay is exponential it is possible to compute the factors that control it based on the general exponential equation:

[2.2] $$e^{-\lambda\Psi t} = W/W_o$$

where: e = natural log, λ = decay constant (= 0.139), Ψ = temperature constant , σ = scavenger constant, t = time for decay (in days), W = weight after decay, W_o = weight before decay.

The decay constant was calculated as follows. The experiments were carried out at an average temperature of 31°C. Therefore Ψ is treated as a value of 1 (Table 2.5 and Appendix 2) and is removed from the equation. This leaves the following simplified equation:

[2.3] $$e^{-\lambda t} = W/W_o$$

By reading a value for W/W_o and for t off the graph, and entering these into Equation 2.3 it is possible to calculate a value for λ.

Temperature affects the rate of decay. Swift *et al.* (1979) stated that the rate of decay doubles when the temperature is increased by 10°C and conversely halves when the temperature is decreased by 10°C. The experiments described here were carried out with an average water temperature of 31°C. A temperature constant (ψ) can therefore be inserted into the equation to predict the effect of temperature change (Table 2.5 and Appendix 2).

Water Temp. °C	Ψ
1	0.125
11	0.250
21	0.500
31	1.000
41	2.000
51	4.000

TABLE 2.5 **The relationship between water temperature and the temperature constant (ψ). See Appendix 2 for a full table of the relationship.**

The mathematical relationship deduced can be applied to a comparison with fossil material. To calculate the duration of decay before burial several values must be inserted in the equation. These are: ψ and W/W_o. The first unknown is ψ, which is dependant on temperature (Appendix 2). It is therefore necessary to obtain the palaeo-temperature for the sea water in the ancient sedimentary environment. The palaeo-temperature from sediments (especially marine sediments) can be obtained by oxygen isotope studies of microfossil tests (see Brasier, 1980 for further details). This system provides accurate values for Cenozoic sediments, and as most avian fossils are from this period, it is possible to obtain a reliable palaeo-temperature data and hence a value for ψ. The final unknown factor is W/W_o. This can only ever be a best guess for a fossil organism, but by estimating the original mass of the bird and then by estimating the weight of the skeleton before fossilisation (by comparison with modern avian skeletons) a value for W/W_o can be obtained. This W/W_o value represents a minimum because no allowance for soft tissue has been made, but a comparison with equivalent modern skeletal material with soft tissue attached allows a second, maximum value for W/W_o to be obtained.

With all these values placed into Equation 2.2 it is possible to derive an estimate for t (time in days). The two values of W/W_o (a maximum and minimum value) yield two values of t (t_{min} and t_{max}). These two values give an estimated range of time (in days) during which the fossil decayed prior to being buried.

Day	1	2	3	4	5	6	7	8	9	10	11
Date	30/6/91	1/7/91	2/7/91	3/7/91	4/7/91	5/7/91	6/7/91	7/7/91	8/7/91	9/7/91	10/7/91
Time	12.15	11.20	11.20	11.30	10.50	11.10	11.15	10.30	10.25	10.35	10.30
Air temp. °C	30	34	35	36	34	35	33	34	35	40	37
Water temp. °C	28	31	33	31	30	31	29	30	30	31	32
Current speed m/s	0.08	0	0.03	0	0	0	0	0	0	0	0
Current direction °	000	N/A	315	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Salinity ppt.	16	16.5	16.5	16.5	17	18	20	19	20	20	23
O_2 content ppm	9.5	9	9	9	9	9.5	9	9	9	10	9.5
pH	7.86	7.8	7.75	7.6	7.24	7.36	7.62	7.45	7.57	7.52	8.4
Water depth m.	0.31	0.31	0.31	0.28	0.26	0.25	0.26	0.25	0.23	0.20	0.20
weather	rain	cloud	sun	sun	sun	sun	sun	sun	sun	sun	sun
Day	20/1	21/2	22/3	23/4	24/5	25/6	26/7	27/8	28/9	29/10	30/11
Date	19/7/91	20/7/91	21/7/91	22/7/91	23/7/91	24/7/91	25/7/91	26/7/91	27/7/91	28/7/91	29/7/91
Time	10.45	9.50	8.55	9.00	8.40	8.50	9.05	8.55	9.10	9.00	11.15
Air temp. °C	33	33	35	34	33	33	29	33.5	33	32	35
Water temp. °C	30	27	31	30	27.5	27	28	27.5	28	27.5	28.5
Current speed m/s	0	0	0	0	0	0	0	0	0	0	0
Current direction °	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Salinity ppt.	20	20	20	20	20.5	21	22	23	21	22	20
O_2 content ppm	10	9	9	9	8.5	9	9	9	9	9	9
pH	8.19	7.28	7.95	--	7.18	7.89	7.63	7.57	7.63	7.68	7.76
Water depth m.	0.24	0.2	0.22	0.21	0.2	0.2	0.21	0.21	0.21	0.21	0.2
weather	cloud	cloud	sun	sun	sun	sun	cloud	sun	cloud	cloud	sun

Table 2.1 Environment data for Freshwater Site, Everglades Swamp, Dade County, Florida

Day	31/12	48/29	57	71
Date	30/7/91	16/8/91	25/8/91	8/9/71
Time	8.05	12.16	10.03	9.46
Air temp. °C	31	38	37	29
Water temp. °C	27.5	34	31	28
Current speed m/s	0	0	0	0
Current direction °	N/A	N/A	N/A	N/A
Salinity ppt.	22	20	20	20
O_2 content ppm	9	9	9	9
pH	7.62	7.36	7.6	7.53
Water depth m.	0.2	0.19	0.19	0.26
weather	cloud	sun	sun	cloud

Table 2.1 cont. Environment data for Freshwater Site, Everglades Swamp, Dade County, Florida

Day	1	2	3	4	5	6	7	8	9	10	11
Date	30/6/91	1/7/91	2/7/91	3/7/91	4/7/91	5/7/91	6/7/91	7/7/91	8/7/91	9/7/91	10/7/91
Time	13.00	12.00	12.00	12.10	11.30	11.50	12.00	11.10	11.00	11.15	11.05
Air temp. °C	28	33	31	35	36	34	37	35	37	42	38
Water temp. °C	30	30	30	31	31	30	32	31	31	32	32
Current speed m/s	0.02	0.02	0.025	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Current direction °	355	340	005	330	330	340	335	340	330	330	340
Salinity ppt.	34	33	34	33	33	33	33	33	33	33	33
O_2 content ppm	12.5	12	12.5	12	12.5	12	12.5	12	12	12	6.3
pH	8.19	8.13	8.07	8.0	8.06	8.14	8.01	8.09	7.99	7.94	8.24
Water depth m.	0.45	0.47	0.46	0.44	0.43	0.41	0.42	0.40	0.39	0.35	0.3
weather	rain	cloud	rain	sun	sun	sun	sun	sun	sun	sun	sun
Day	20/1	21/2	22/3	23/4	24/5	25/6	26/7	27/8	28/9	29/10	30/11
Date	19/7/91	20/7/91	21/7/91	22/7/91	23/7/91	24/7/91	25/7/91	26/7/91	27/7/91	28/7/91	29/7/91
Time	12.00	10.30	9.40	9.40	9.25	9.20	9.35	9.45	9.50	9.40	11.45
Air temp. °C	35	37	35	35	33	32	28	36.5	34	34	35
Water temp. °C	38	30	32	31	30	30	29	29	30	30	32
Current speed m/s	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.005	0.01	0.005	0.02
Current direction °	300	300	310	310	100	180	330	340	330	325	355
Salinity ppt.	32	34	33	33	33.5	32	33	32	33	33	32
O_2 content ppm	7.8	7.8	8.0	8.0	7.8	7.8	8.5	8	8	8	8
pH	8.43	8.21	8.07	--	8.11	8.06	8.08	8.13	8.18	8.25	8.32
Water depth m.	0.25	0.28	0.26	0.27	0.28	0.25	0.26	0.245	0.25	0.25	0.25
weather	cloud	sun	sun	sun	cloud	cloud	rain	sun	cloud	cloud	sun

Table 2.1 cont. Environment data for Seawater Site, Crocodile Ponds, Monroe County, Florida

Day	31/12	48/29	57	71
Date	29/7/91	16/8/91	25/8/91	8/9/91
Time	8.50	13.04	10.53	10.21
Air temp. °C	31	43	41	30
Water temp. °C	28.5	37	35	31
Current speed m/s	0.02	0	0.01	0.01
Current direction °	355	N/A	330	330
Salinity ppt.	30	33	33	33
O_2 content ppm	8	7.8	8	8
pH	8.19	7.28	8.09	8.03
Water depth m.	0.27	0.19	0.27	0.36
weather	cloud	sun	sun	cloud

Table 2.1 cont. Environment data for Seawater Site, Crocodile Ponds, Monroe County, Florida

Common Name	*Scientific Name*	Numbers of Specimens	Size Category
Double Crested Cormorant	*Phalacrocorax auritus*	12	Large
Brown Pelican	*Pelecanus occidentalis*	6	Large
Laughing Gull	*Larus atricilla*	8	Large
Great Northern Diver	*Gavia immer*	1	Large
Royal Tern	*Sterna maxima*	1	Large
Sooty Tern	*S. fuscata*	1	Large
Audubon Shearwater	*Puffinus lherminieri*	2	Large
Osprey	*Pandion haliaetus*	1	Large
Ringed Turtle Dove	*Streptopelia risoria*	5	Small
Mourning Dove	*Zenaida macroura*	1	Small
Blue Jay	*Cyanocitta cristata*	1	Small
Red Bellied Woodpecker	*Melanerpes carolinus*	1	Small
Northern Cardinal	*Richmondena cardinalis*	1	Small
Yellow Warbler	*Dendroica tigrina*	1	Small
Yellow Throated Warbler	*D. dominica*	1	Small
Black Throated Blue Warbler	*D. coerulescens*	1	Small
White Crowned Pigeon	*Columba leucocephala*	5	Small
American Kestrel	*Falco sparverius*	1	Small
Belted Kingfisher	*Ceryle alcyon*	1	Small
Common Nighthawk	*Chordeiles minor*	1	Small
Eastern Screech Owl	*Otus asio*	1	Small
Wilsons Plover	*Charadrius wilsonia*	1	Small
Ovenbird	*Seirus aurocapillus*	6	Small
Louisiana water thrush	*S. motacilla*	1	Small
Common Yellow Throat	*Geothlypis trichas*	1	Small
American Redstart	*Setophaga ruticilla*	1	Small
Red Eyed Vireo	*Vireo olivaceus*	1	Small

TABLE 2.2 **Species, sizes and numbers of specimens used in the actualistic decay experiments.**

Experiment	Environment	Size of specimen	Protected	Expt. Code
1	Freshwater	Large	Yes	FLP
2	Freshwater	Large	No	FLUP
3	Freshwater	Small	Yes	FSP
4	Freshwater	Small	No	FSUP
5	Sea-water	Large	Yes	SLP
6	Sea-water	Large	No	SLUP
7	Sea-water	Small	Yes	SSP
8	Sea-water	Small	No	SSUP

TABLE 2.3 **Classification of experiments conducted within the two field sites.**

Name	Number	Description of specimen	Description of Pyrite	a Diam. (mm)	b Diam. (mm)	area (mm^2)
Precursor parvus	A 3684	Distal end of left humerus	Crystalline pyrite coating endiosteal surface	1.7	2.2	11.75
Precursor parvus	A3553	Proximal end of left humerus	Amorphous pyrite filling medullary cavity with crystalline pyrite coating endiosteal surface	1.6	2.0	10.05
Precursor magnus	A3683	Distal end of right tarsometatarsus	No pyrite	-	-	-
cf. Precursor magnus	A4356	Proximal end of left carpometacarpus	Amorphous pyrite filling medullary cavity	2.1	2.5	16.49
Precursor litorum	A3135	Distal end of right humerus	Amorphous pyrite filling medullary cavity	3.4	3.55	37.92
cf. Precursor	A5180	Proximal end of left carpometacarpus	No pyrite	-	-	-
Promuso-phaga sp.	A43165	Proximal end of left femur	Crystalline pyrite coating endiosteal surface	5.6	6.3	110.8
Promuso-phaga magnifica	A33138	Proximal end of left humerus	Amorphous pyrite filling medullary cavity	6.6	8.3	172.1
Promuso-phaga magnifica	A38935	2 broken shafts of a right and left humeri	Crystalline pyrite coating endiosteal surface	4.5 6.6	5.25 8.8	74.22 182.5
Promuso-phaga magnifica	A38934	Broken rib shaft	Crystalline pyrite coating endiosteal surface	-	-	-
Parvicuc-ulid	A5291	Distal left humerus	Amorphous pyrite filling medullary cavity	1.5	1.8	8.48
Parvicuc-ulid	A3311	Proximal right carpometacarpus	Amorphous pyrite filling medullary cavity	1.0	1.4	4.4
Prionapus lacki	A2166	Left humerus	? undetectable as bone is not broken	-	-	-

Table 2.4 **Descriptions of specimens containing pyrite from the Eocene London Clay of S.E. England.**

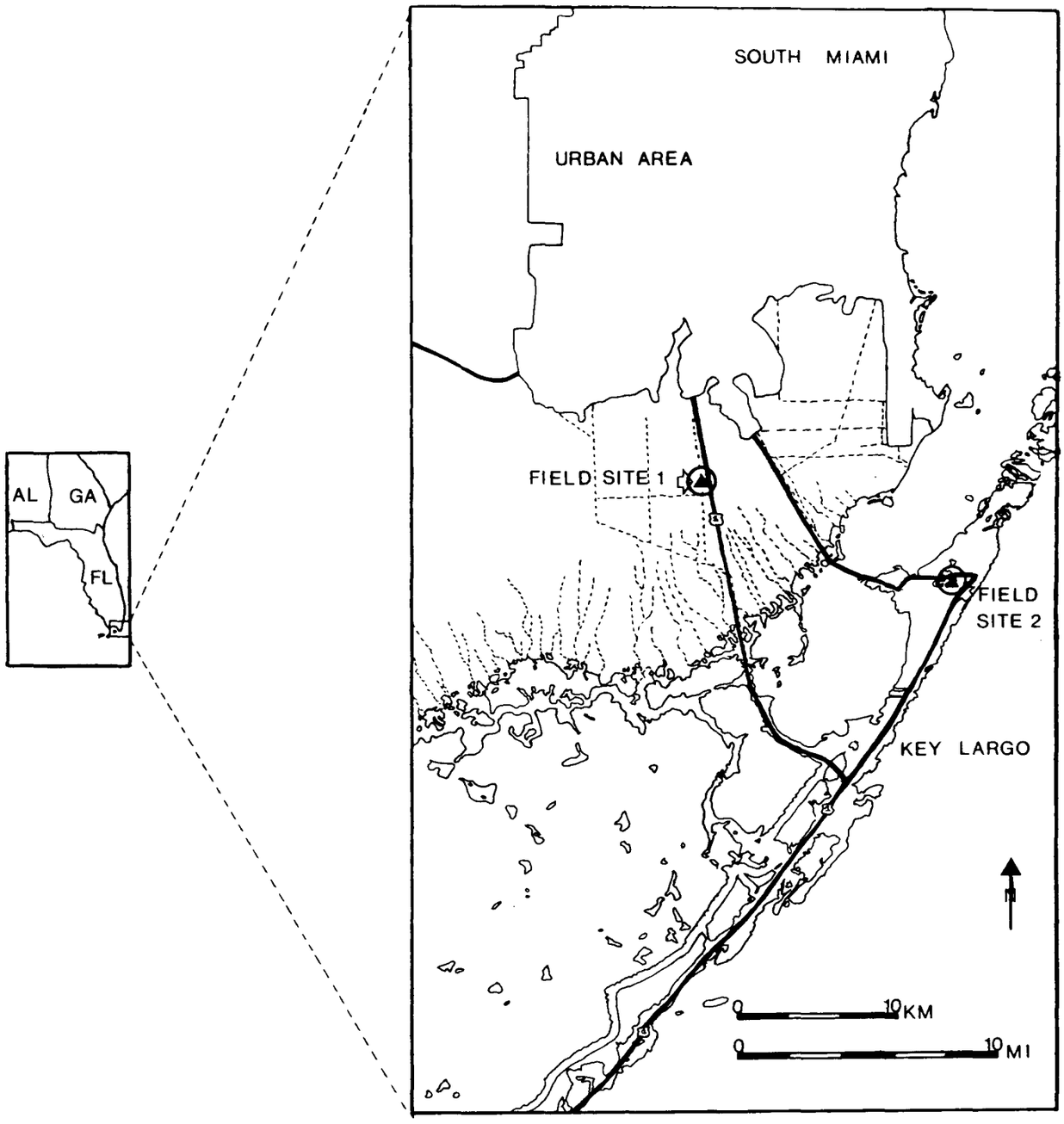


FIGURE 2.1 Southern Florida showing the two field sites. Dotted lines indicate water courses and solid lines indicate major highways.

Figure 2.2. Graph of % weight loss versus time for FLP specimens

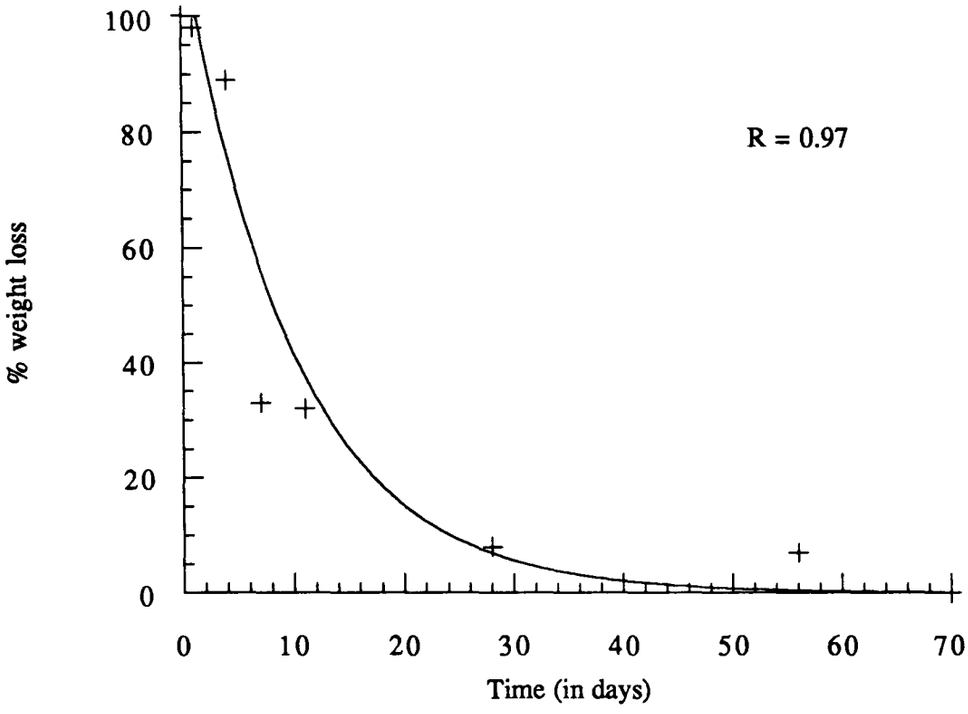


Figure 2.3. Graph of % weight loss versus time for SLP specimens

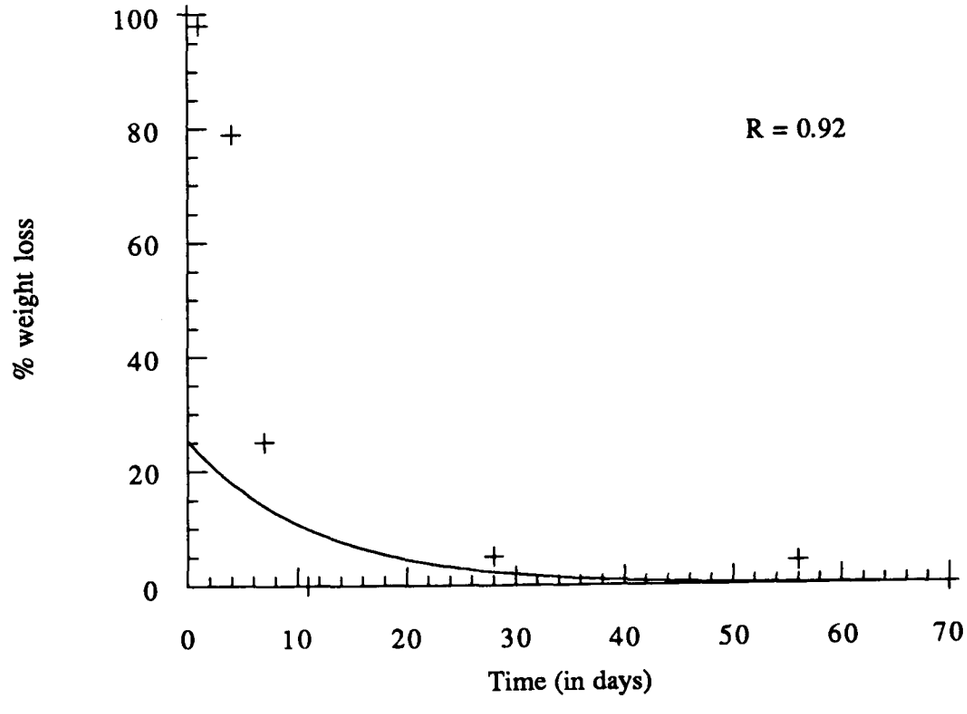


Figure 2.4. Graph of % weight loss versus time for FSP specimens

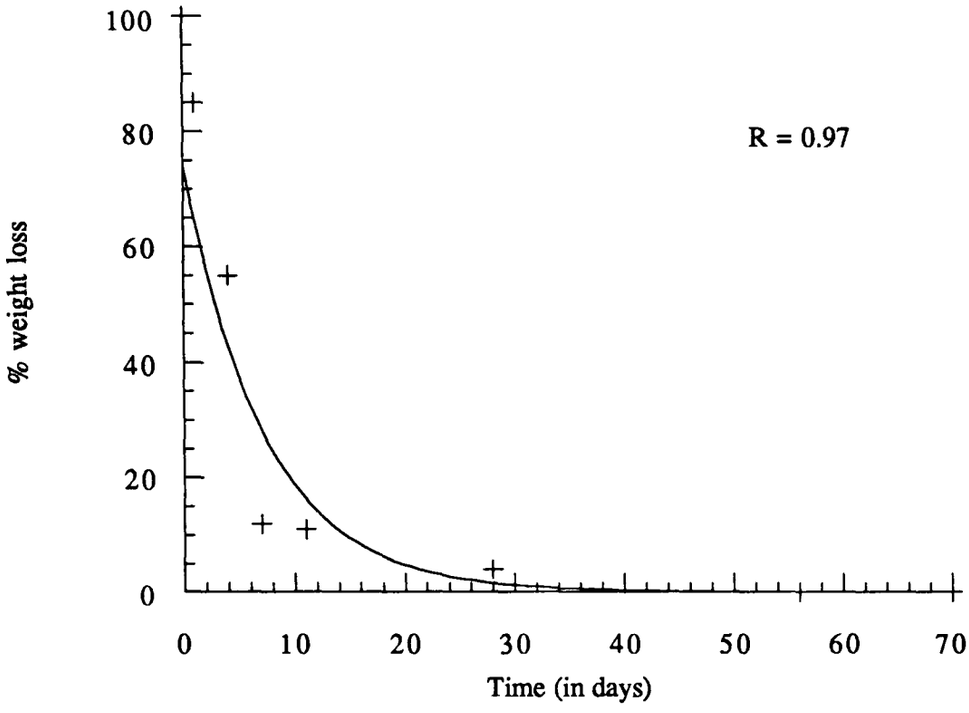


Figure 2.5. Graph of % weight loss versus time SSP specimens

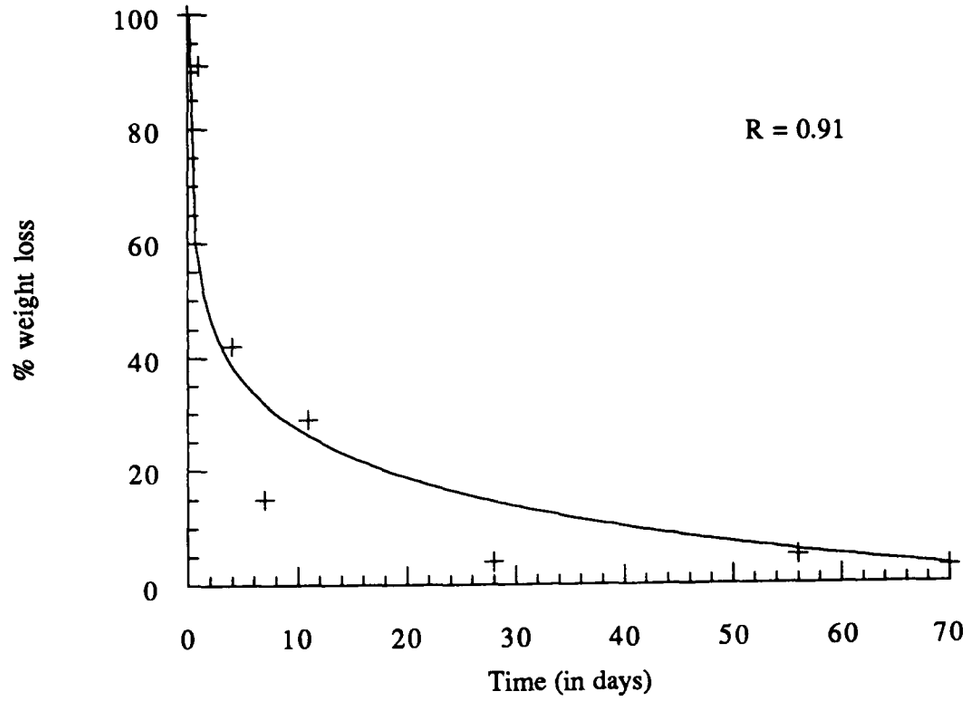


Figure 2.6. Graph of % weight loss versus time for FLUP specimens

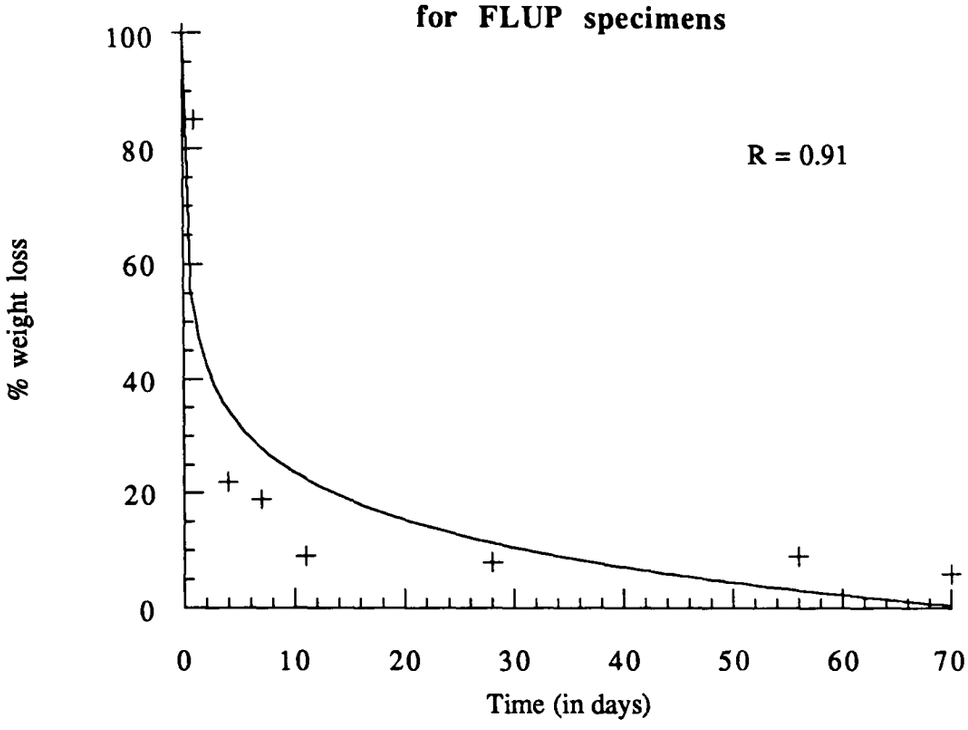


Figure 2.7. Graph of % weight loss versus time for SLUP specimens

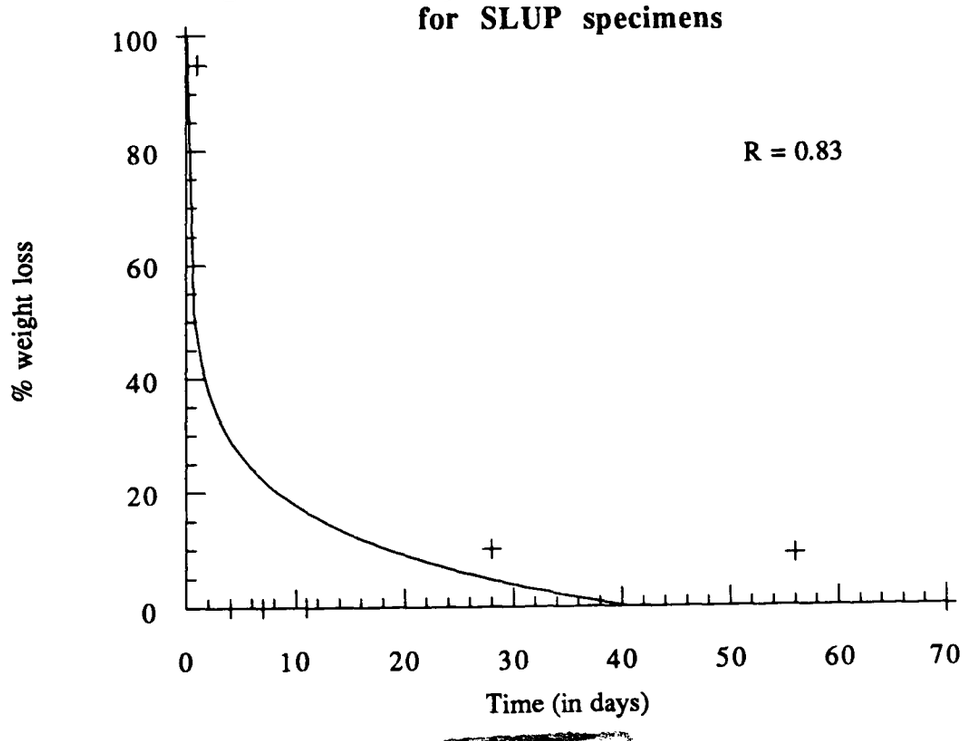


Figure 2.8. Graph of % weight loss versus time for FSUP specimens

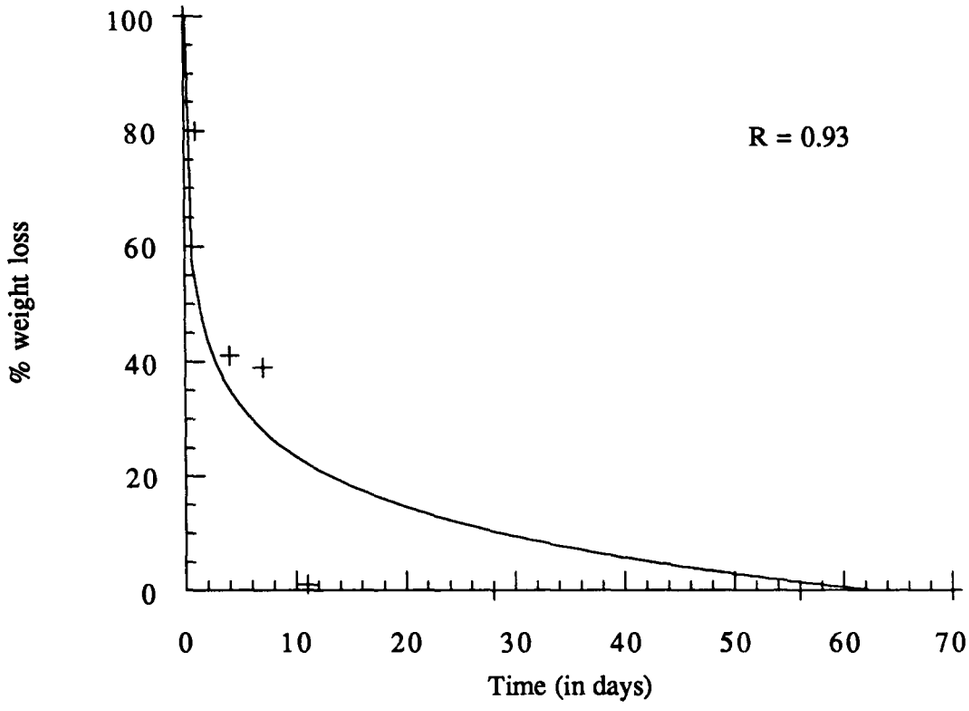


Figure 2.9. Graph of % weight loss versus time for SSUP specimens

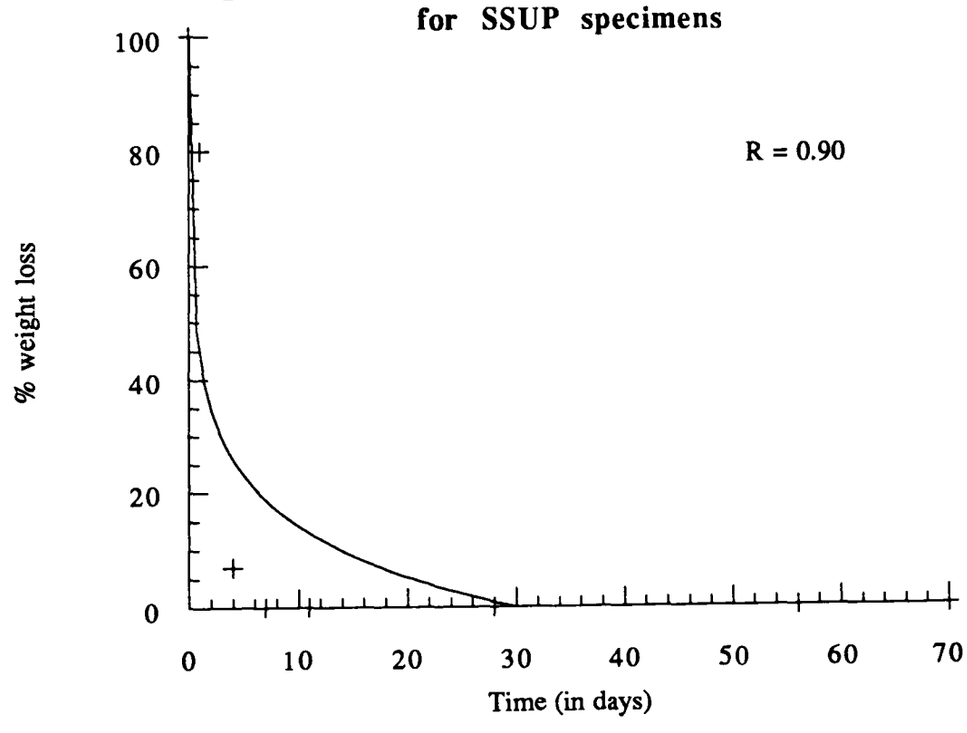


Figure 2.10. Graph of % weight loss for protected specimens

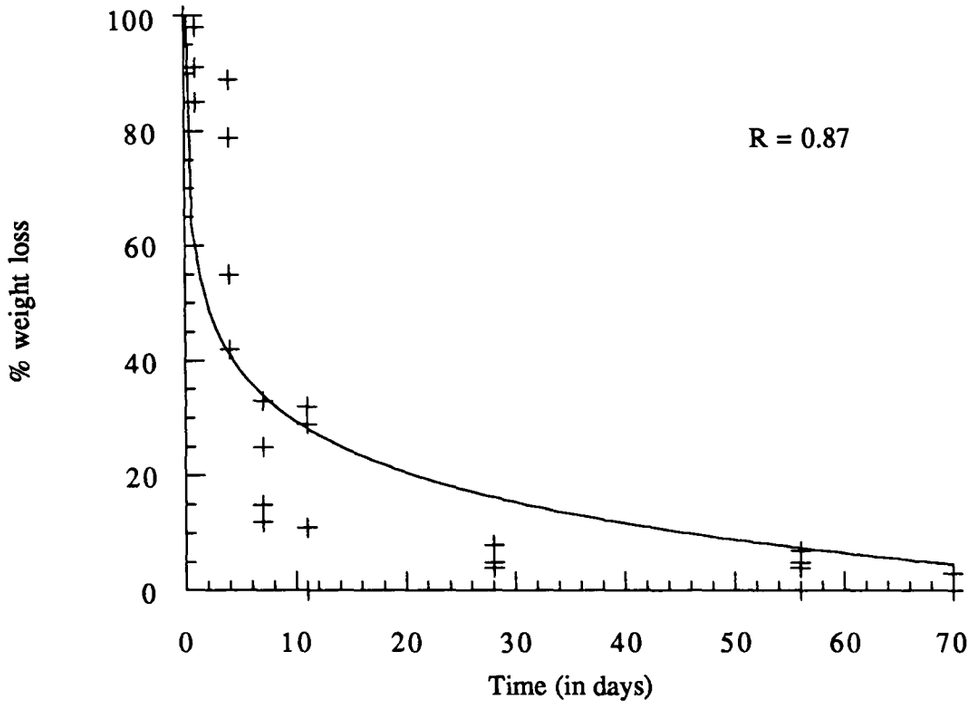


Figure 2.11. Graph of % weight loss versus time for unprotected specimens

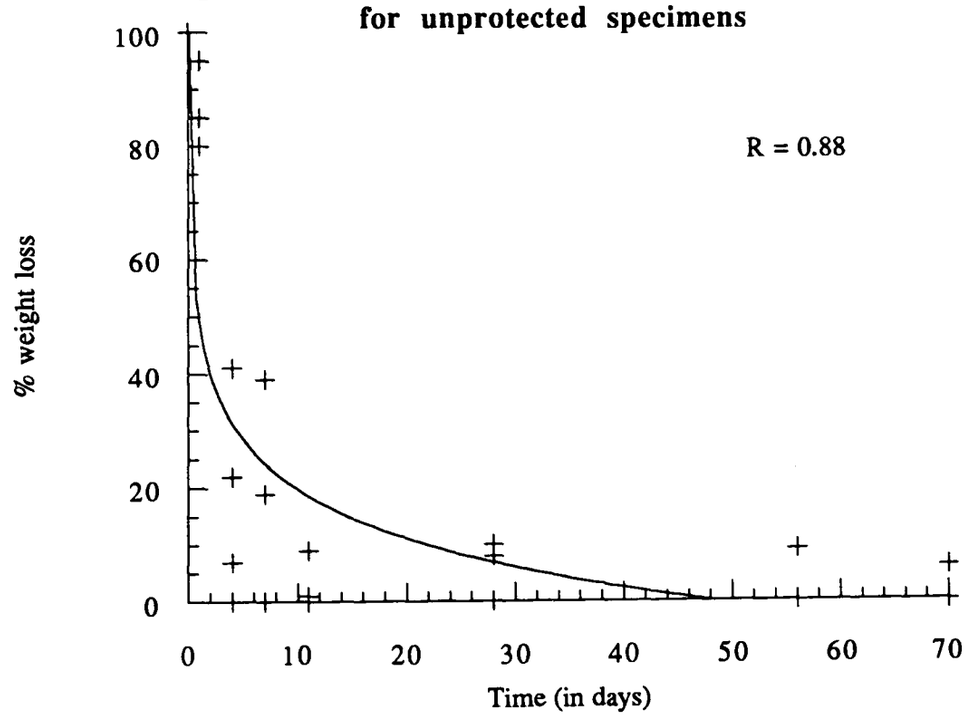


Figure 2.12. Graph of % weight loss versus time for large specimens

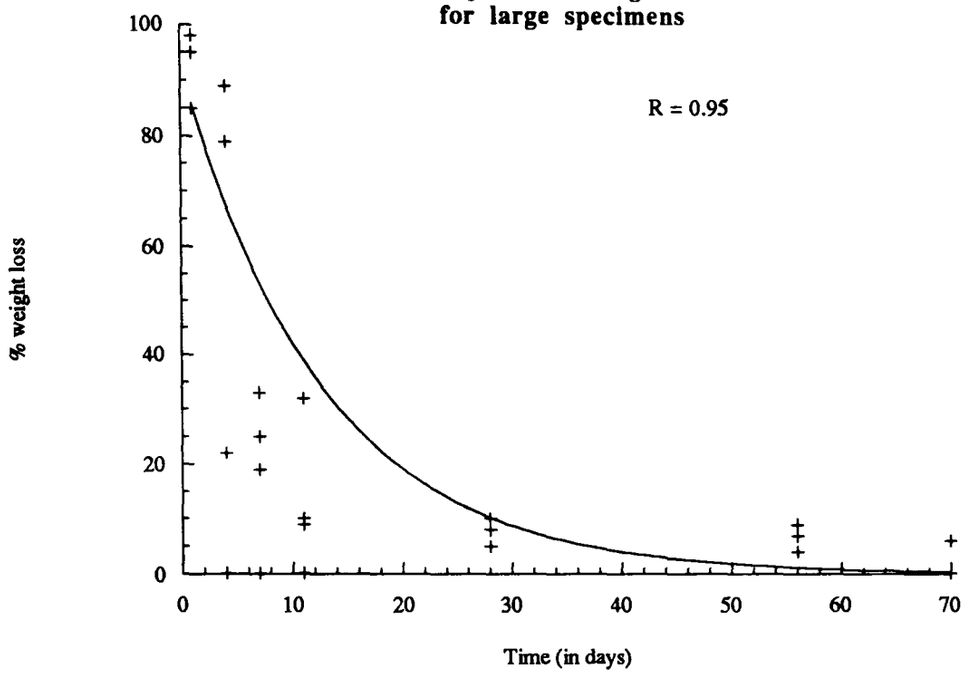


Figure 2.13. Graph of % weight loss versus time for small specimens

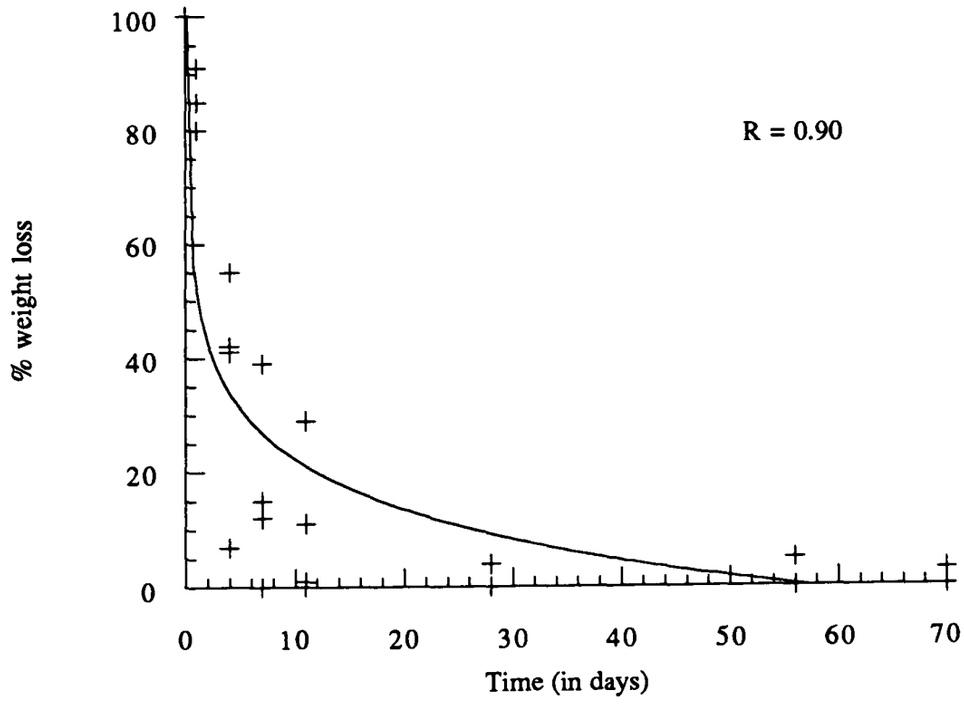


Figure 2.14. Graph of % weight loss versus time for freshwater specimens

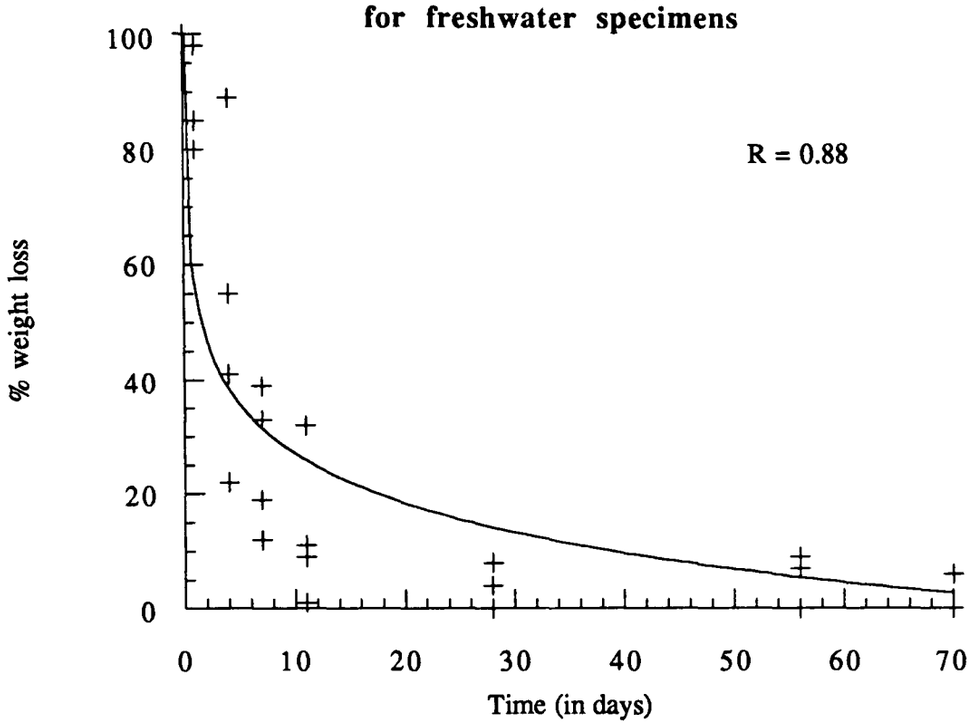


Figure 2.15. Graph of % weight loss versus time for seawater specimens

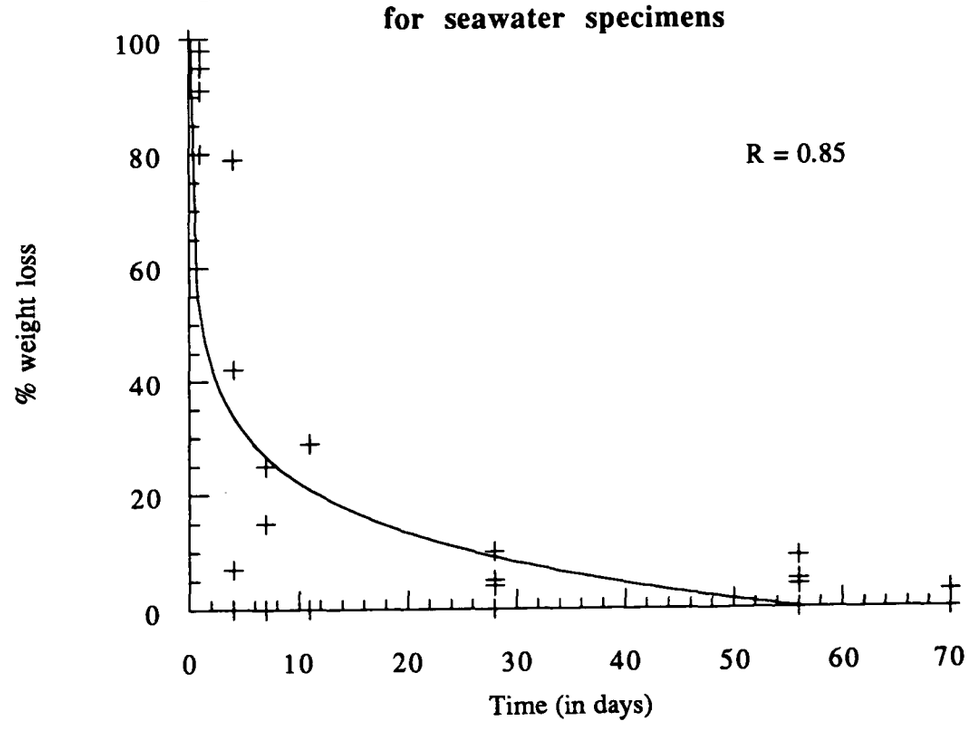


Figure 2.16. Graph of % weight loss versus time for all specimens

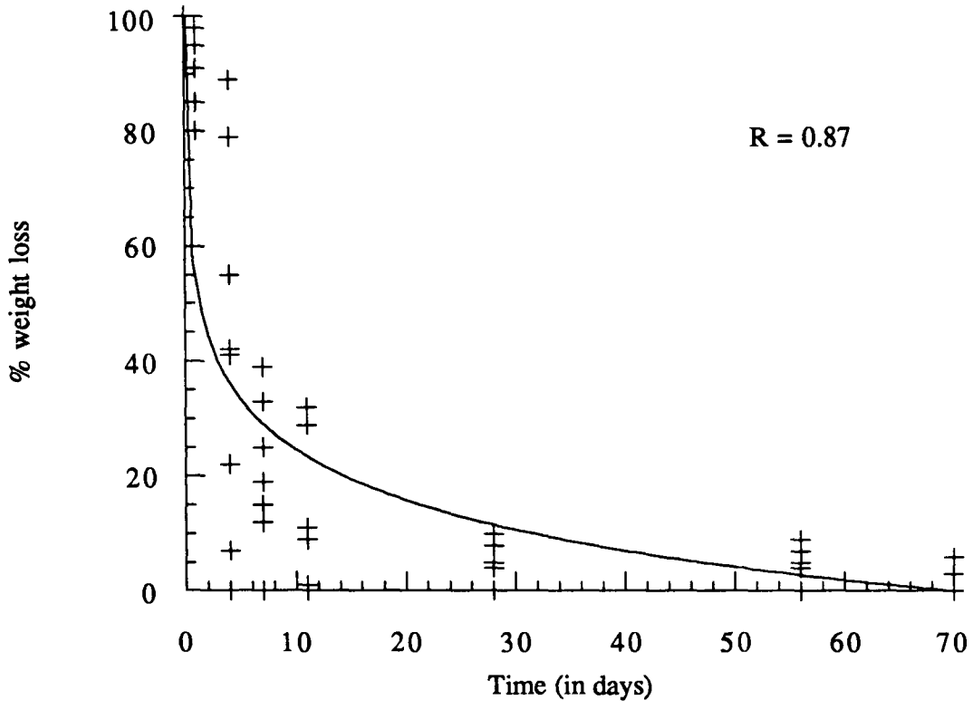


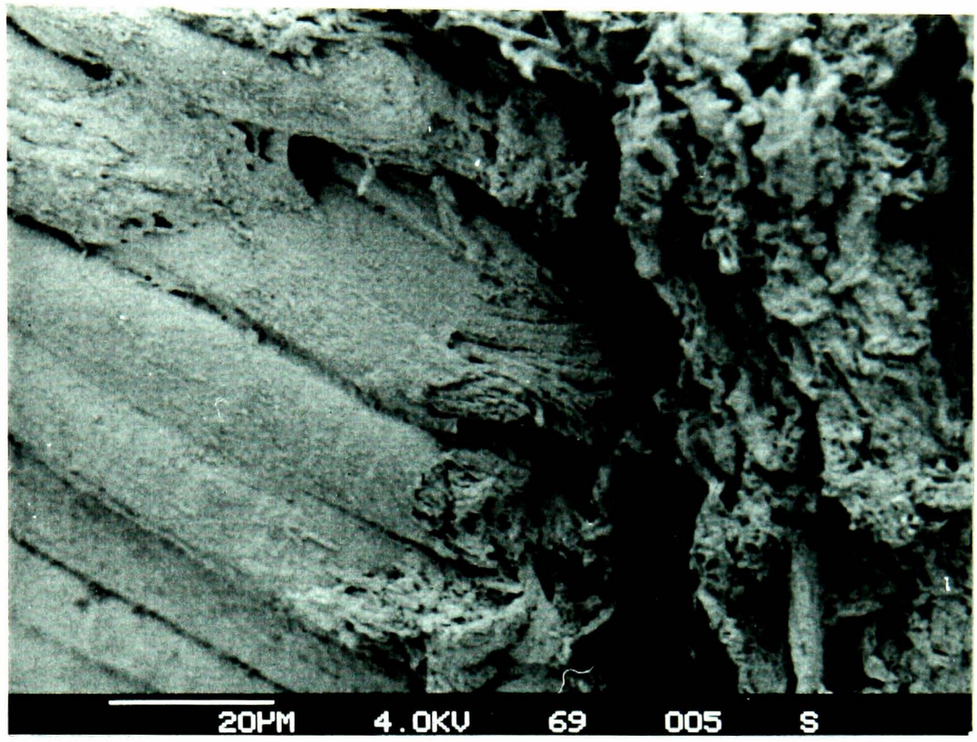
FIGURE 2.17 A leg of a Brown Pelican being scavenged by Crown Conches (*Melongena corona*) in the salt water environment.

FIGURE 2.18 (top)

The pectoralis muscle of an Osprey (*Pandion haliaetus*) after one day of decay. This figure shows that the myoseptum between the muscle blocks has started to decay and separate as a result of the action of autolytic enzymes.

FIGURE 2.19 (bottom)

The pectoralis muscle of an Osprey (*Pandion haliaetus*) after one day of decay. This figure shows that the muscle fibres have started to break into small blocks bounded by the z bands of the muscle. This is also due to the action of autolytic enzymes.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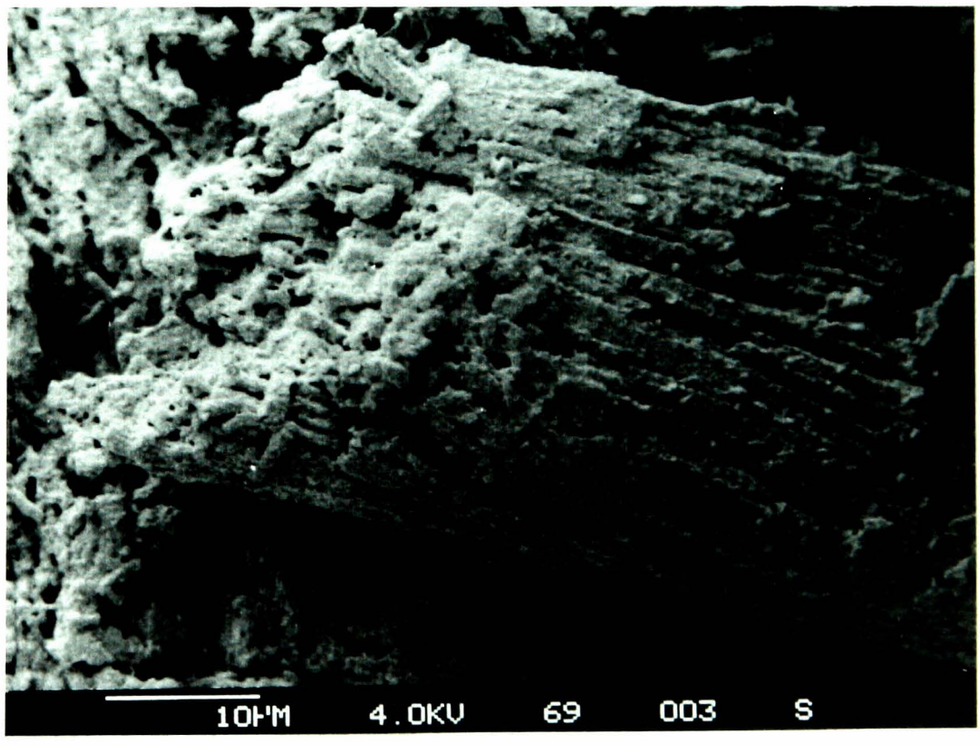
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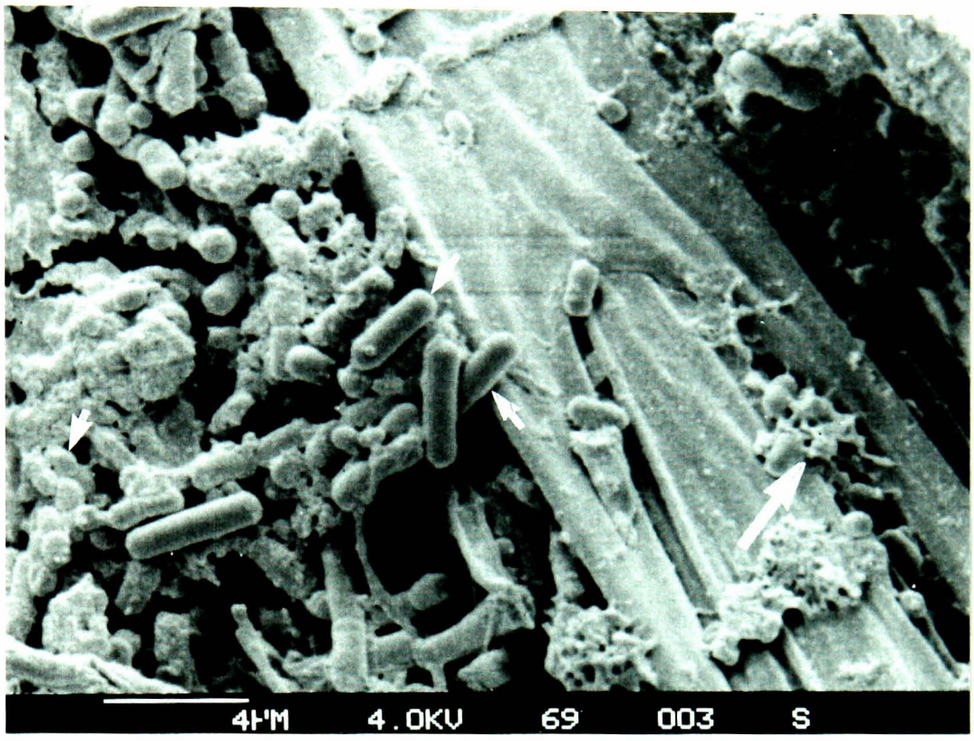
FIGURE 2.20 (top)

Three different morphological types of bacteria on an Osprey muscle after one day of decay. The coccoid types can be seen in the left hand corner of the photograph (arrowed). The two bacilliform types can be seen in the centre of the photograph (arrowed). Note the formation of bacterial glycocalyx (arrowed) which anchor the bacteria to the muscle.

FIGURE 2.21 (bottom)

A fourth morphological type of bacteria (arrowed) identified in an Osprey muscle after one day of decay.


4㎛ 4.0KV 69 003 S

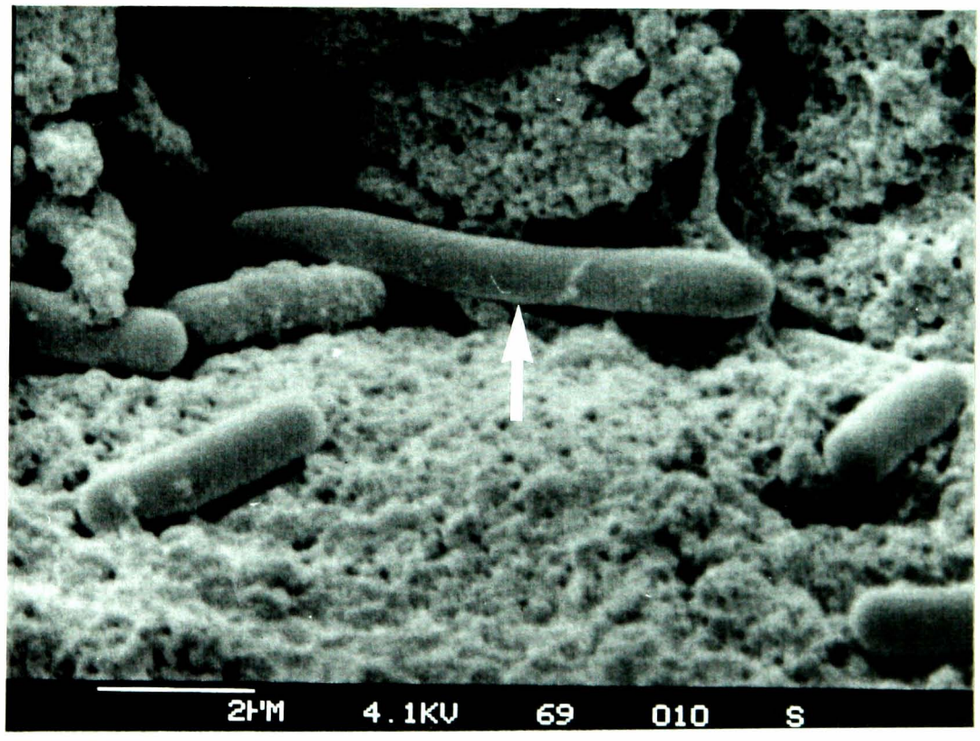

2㎛ 4.1KV 69 010 S

FIGURE 2.22 Laughing gull (*Larus atricilla*) (category FLP) showing morphological decay stage 1. Soft tissues are decaying but still remain cohesive.

FIGURE 2.23 Laughing gull (*Larus atricilla*) (category FLP) showing morphological decay stage 2. The soft tissues have decayed away leaving the feathers shrouding the skeleton.

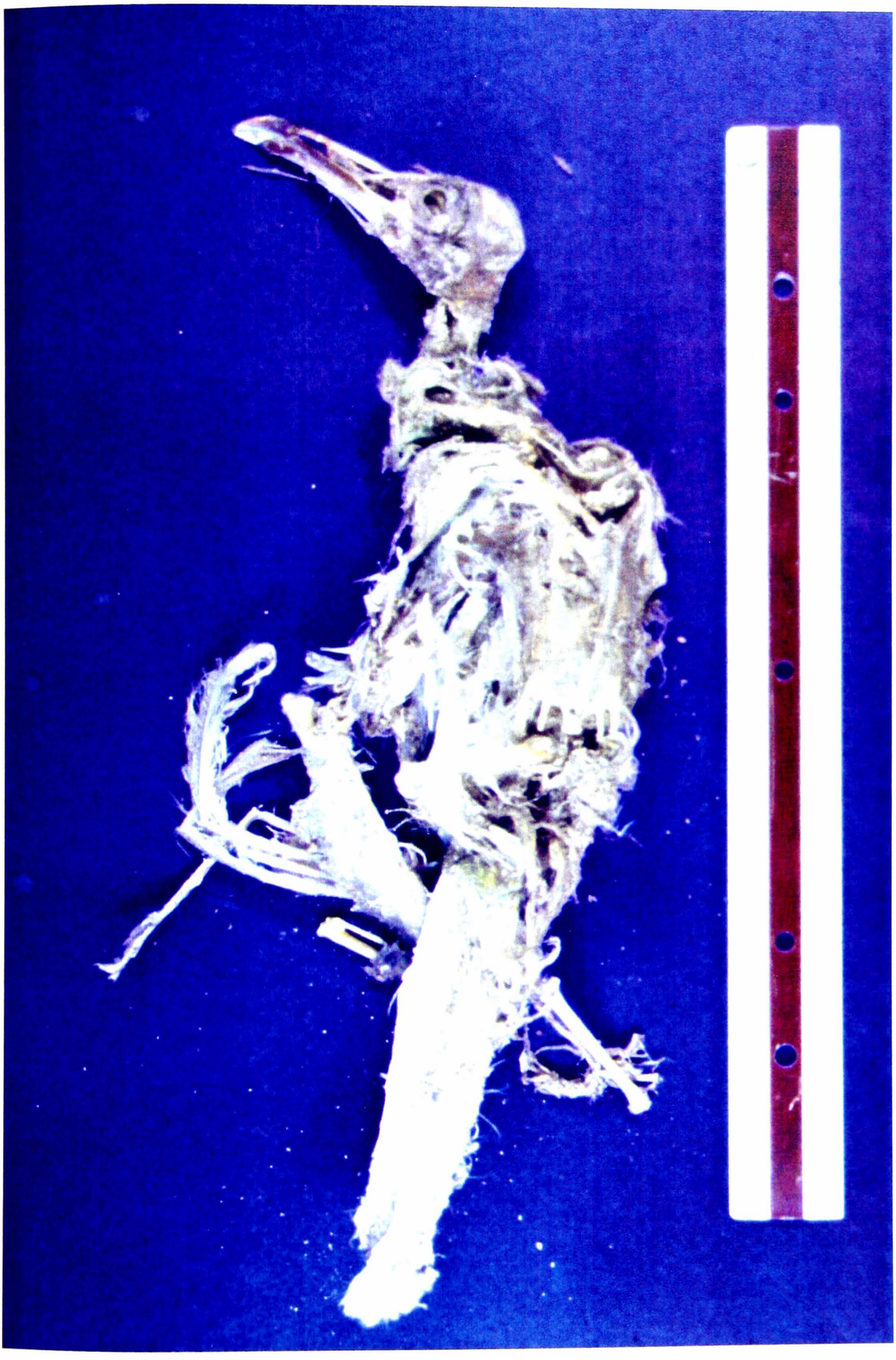


FIGURE 2.24 (Top) Eastern screech owl (*Otus asio*) (category FSUP) showing morphological decay stage 3a. The soft tissues have decayed away and the skull has disarticulated from the cervical vertebrae. Field of view = 20cm.

FIGURE 2.25 (bottom) White crowned pigeon (*Columba leucocephala*) (category FSP) showing morphological decay stage 3b. The legs have disarticulated from the synsacrum articulation but are still in their relative anatomical position due to undecayed skin holding them to the carcass. Field of view = 20cm.

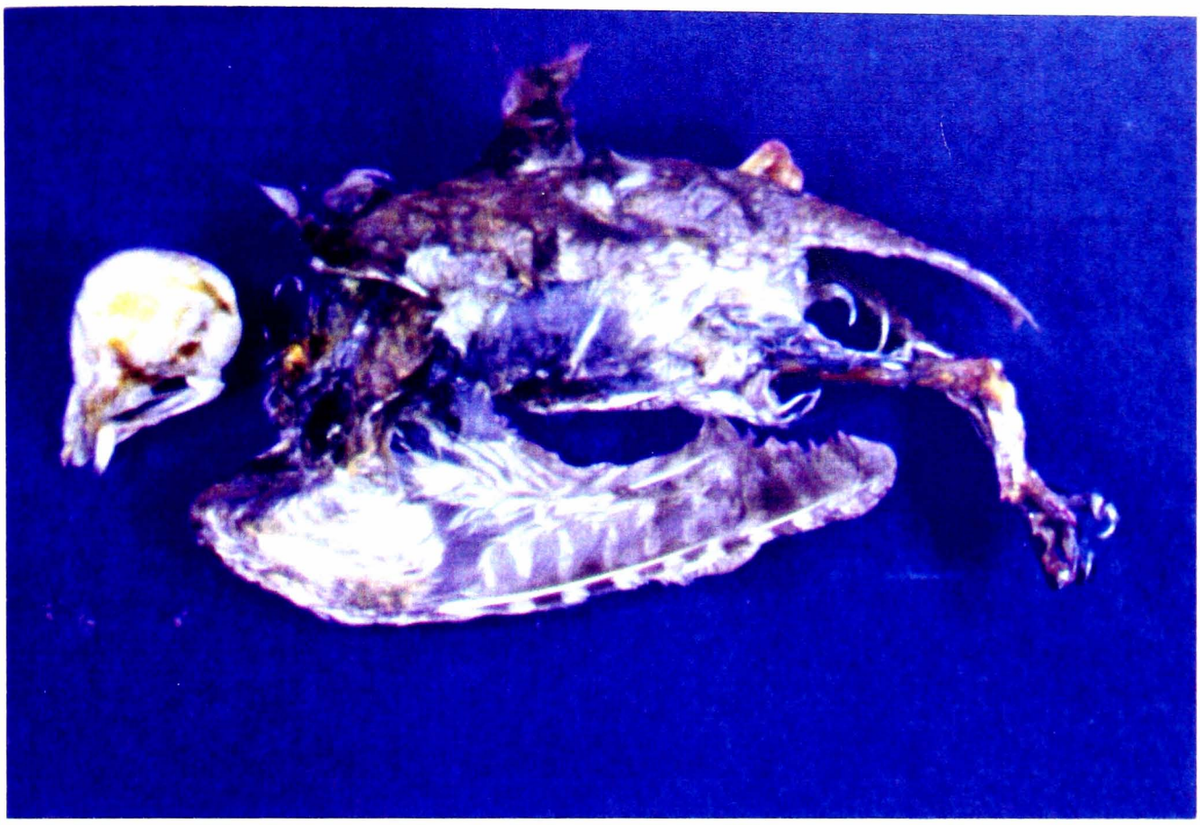


FIGURE 2.26

Belted kingfisher (*Ceryle alcyon*) (category FSUP) showing morphological decay stage 3c. The pectoral girdle (still articulated) has become detached from the rest of the cadaver. In this particular specimen the pectoral girdle was disarticulated from the rest of the skeleton by scavenger action. The scavenger also caused the premature disarticulation of the left wing from the pectoral girdle.

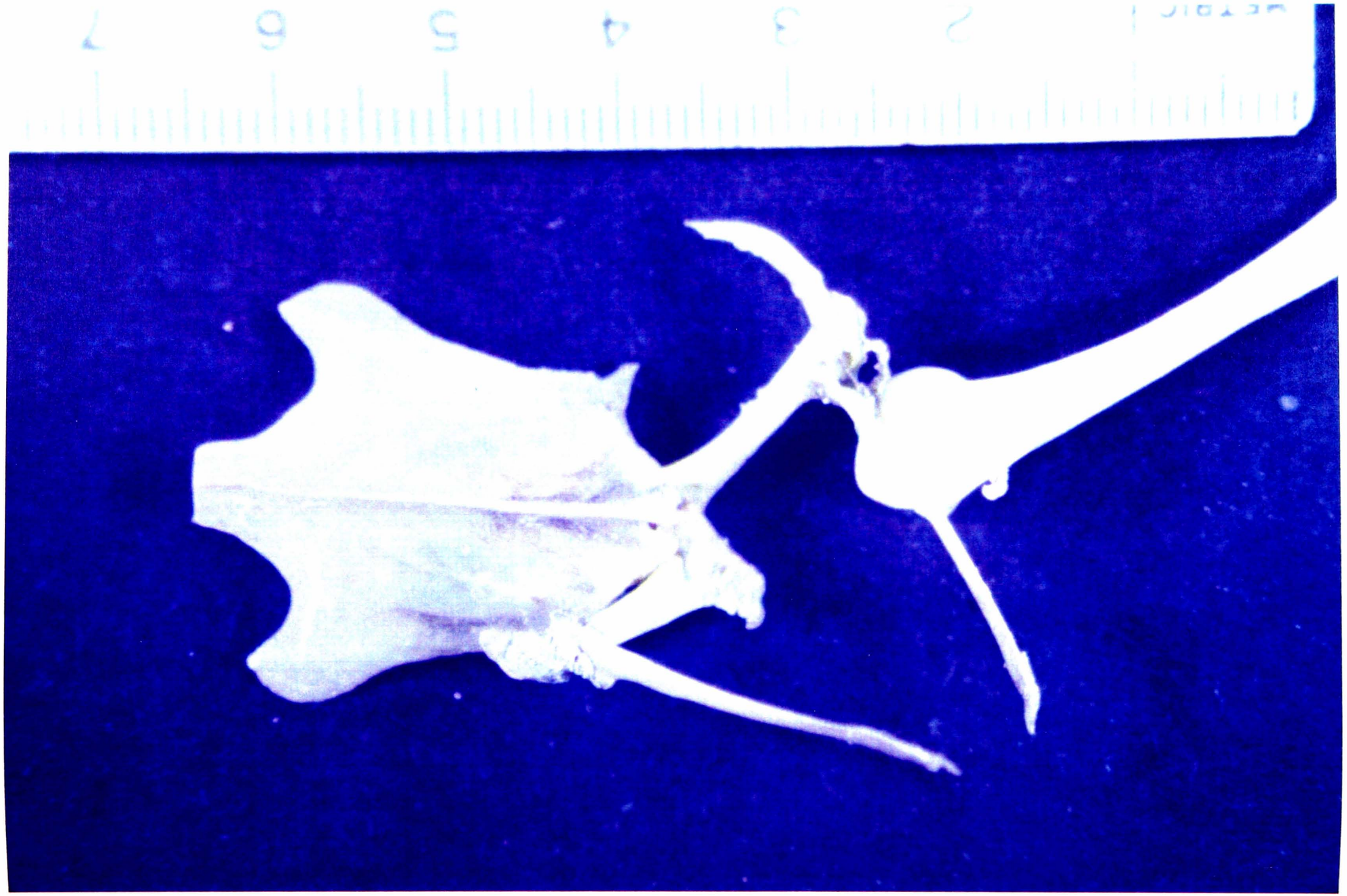


FIGURE 2.27 Laughing gull (*Larus atricilla*) (category FLUP) showing morphological decay stage 3d. The vertebrae in the abdominal region have disarticulated. This has caused the synsacrum to disarticulate from the thorax.

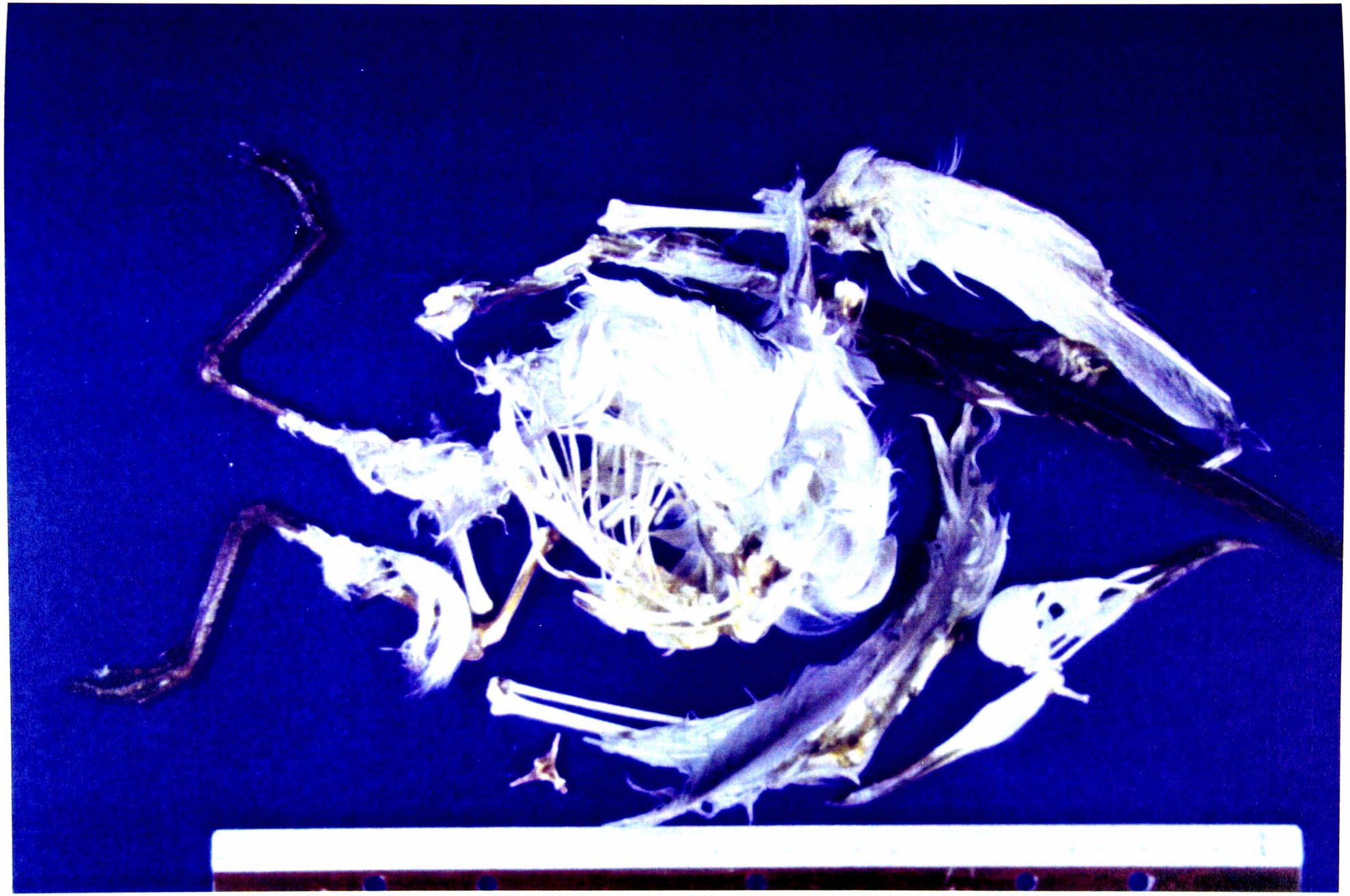
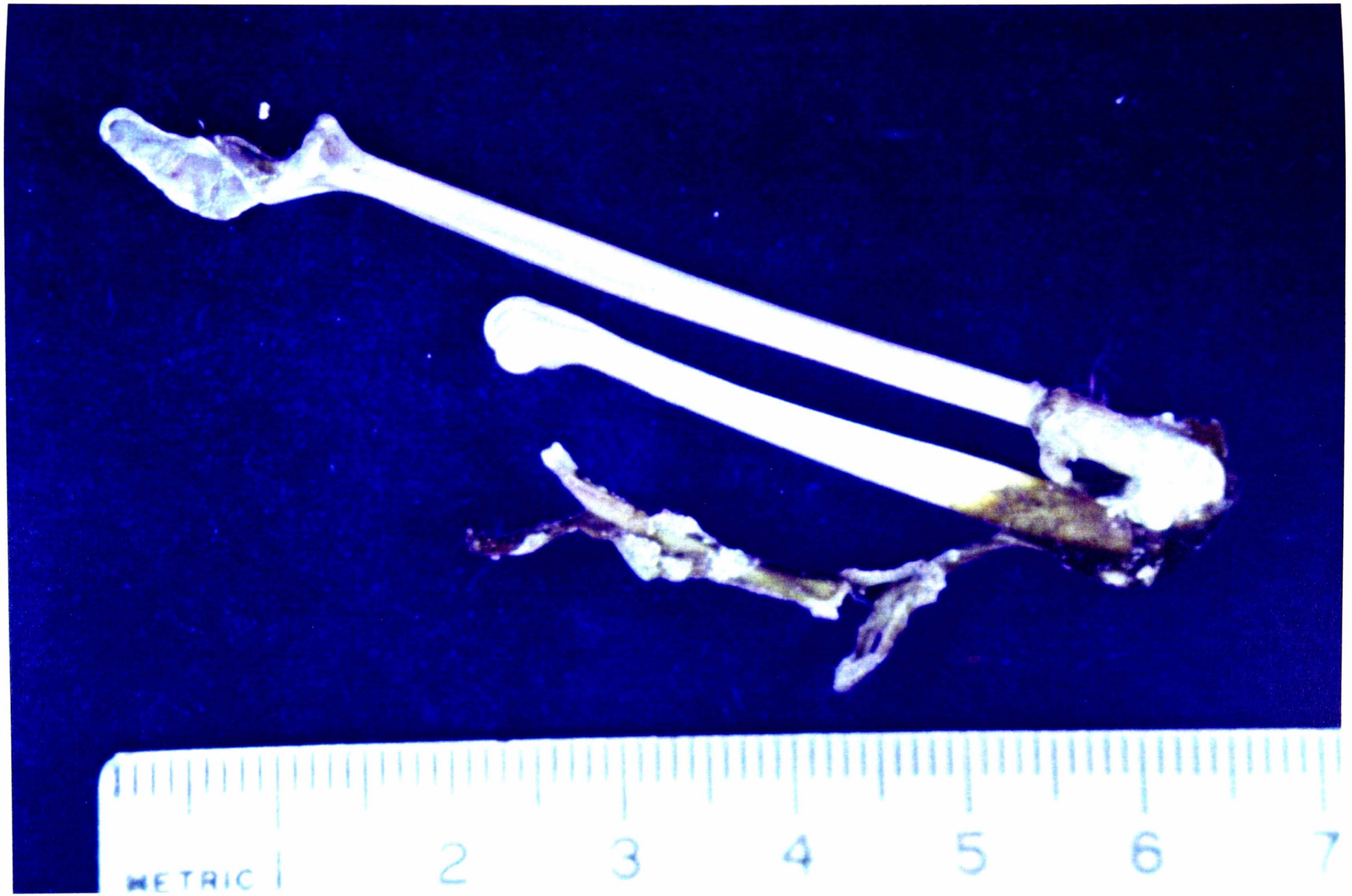


FIGURE 2.28 White crowned pigeon (*Columba leucocephala*) (category FSP) showing morphological decay stage 3e. The thoracic vertebrae have disarticulated and the ribs have separated from their associated vertebrae.

FIGURE 2.29

Audubon shearwater (*Puffinus lherminieri*) (category FLUP) showing morphological decay stage 3f. The legs are disarticulating into individual skeletal elements. In this specimen the leg has disarticulated and only the tibiotarsus and tarsometatarsus remain articulated.


METRIC
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6
7

FIGURE 2.30 Audubon shearwater (*Puffinus lherminieri*) (category FLUP) showing morphological decay stage 3g. The pectoral girdle is separating into distinct elements. In this specimen the humerus, scapula and coracoid remain articulated but have separated from the rest of the pectoral girdle.

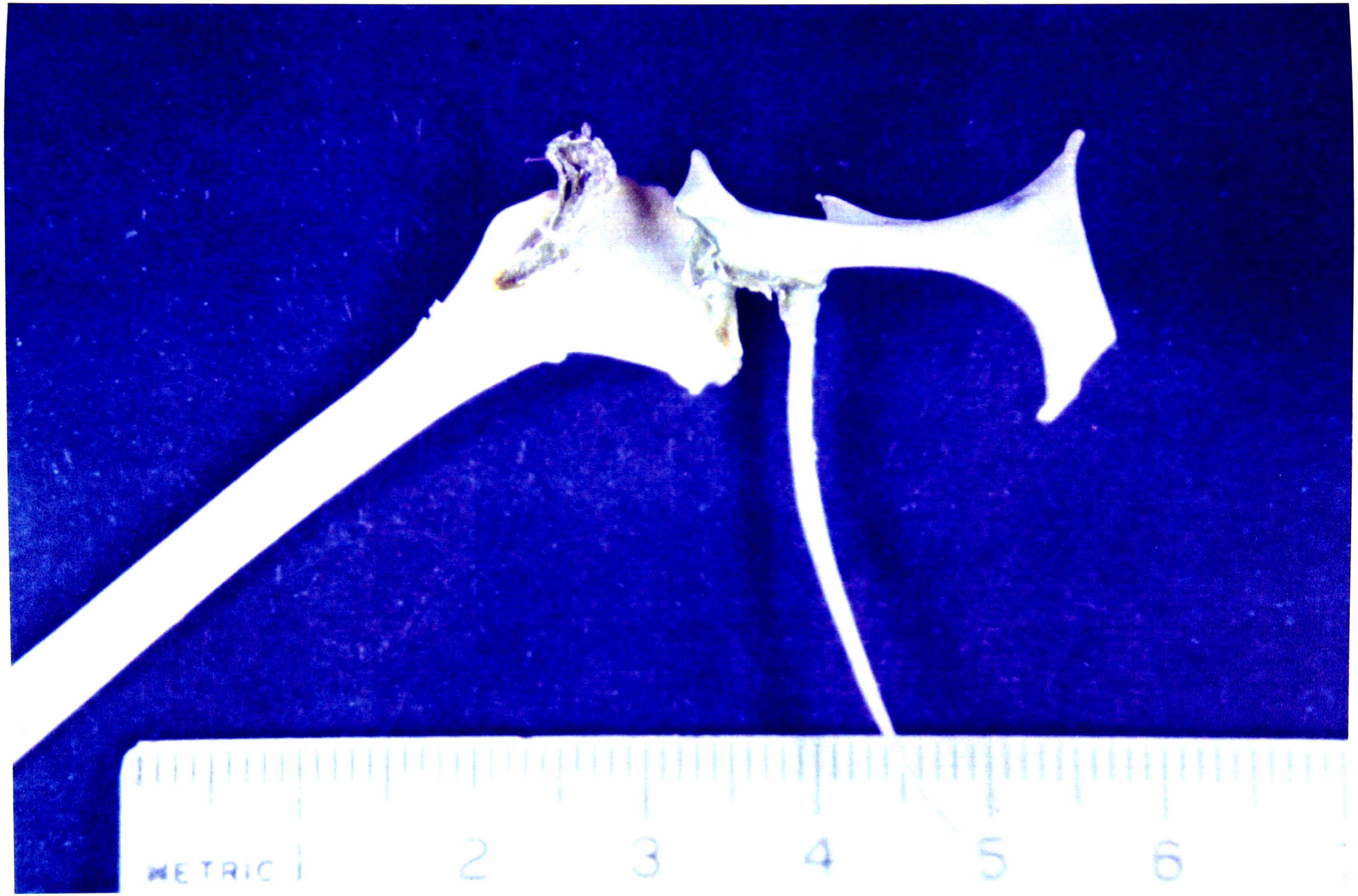
METRIC
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FIGURE 2.31 Royal tern (*Sterna maxima*) (category FLUP) showing morphological decay stage 4. The skeleton is completely disarticulated and the photograph reflects the position of the bones when the specimen was collected from the fieldsite.

FIGURE 2.32 Ovenbird (*Seirus aurocapillus*) (category SSP) showing morphological decay stage 5. The specimen is completely disarticulated and skeletal elements are missing due to their removal by external factors.

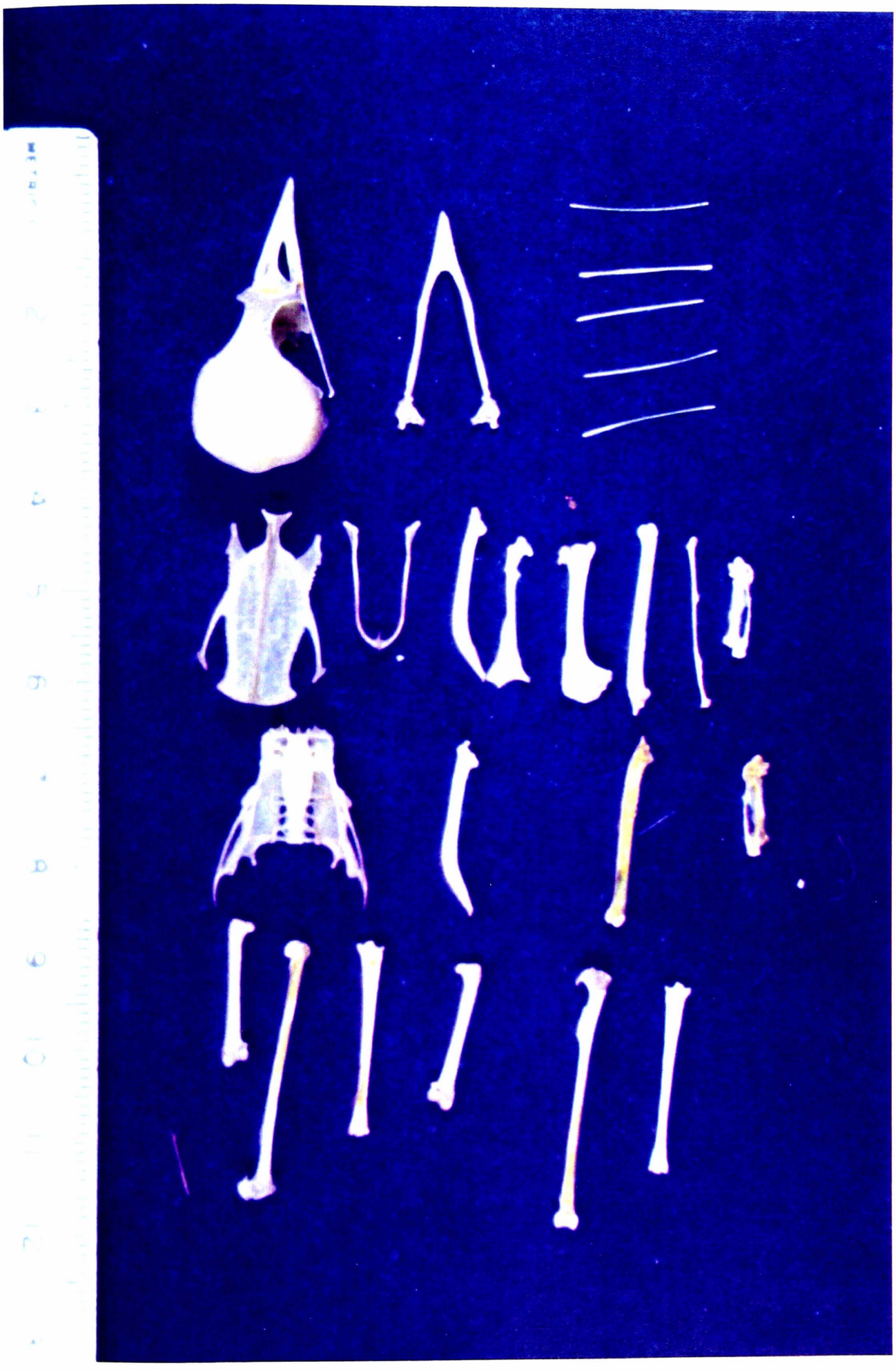
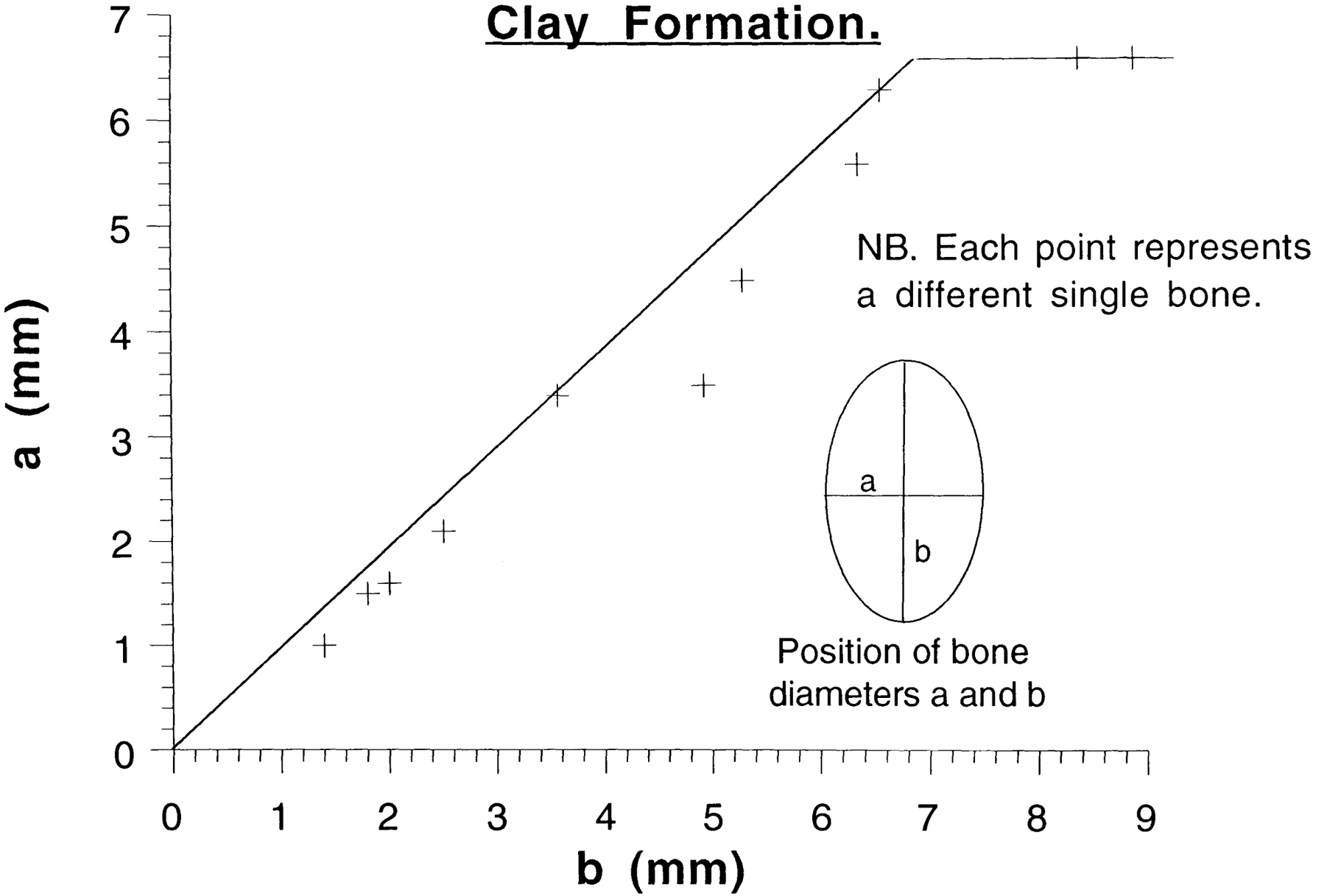


Figure 2.33 Field of Pyrite Formation in bird bones from the Eocene London Clay Formation.



Chapter Three
The Bioerosion of Bird Bones

3a. Introduction

Bioerosion is the abrasion of hard substrates through the activity of organisms (Neumann, 1966). Akpan (1990) classified bioerosional organisms into two groups based on their bioerosional activities:

1. Endolithic cyanobacteria, algae, fungi, insects, clionid and other sponges, phoronids and polychaetes, the activities of which result in partial or complete replacement of solid substrates with voids.
2. Molluscs, fish or regular echinoids, which mechanically abrade substrates through the action of radulae or teeth.

Most of the research into modern and ancient bioerosion has been conducted on the degradation of calcium carbonate substrates such as corals, shells and limestones, resulting in the production of fine fractions of carbonate sediments (Odum and Odum, 1955; Neumann, 1966; Boekschoten, 1966; Hein and Risk, 1975; Perkins and Tsentas, 1976; Bromley, 1978; Torunski, 1979; Farrow and Clokie, 1979; Tudhope and Risk, 1985; Frey and Howard, 1986; Fürsich and Flessa, 1987; Akpan, 1990; Davies et al., 1990; Meldahl and Flessa, 1990).

This study presents a synthesis of evidence for modern, archaeological, and palaeontological bioerosion of vertebrate tissue. It describes the first evidence for the bioerosion of modern, archaeological and fossil bird bones In addition a new form of bioerosion known as Hackett tunnels is identified, and the bioerosion of vertebrate tissue by cyanobacteria and algae is identified for the first time.

3b. Previous Research

There has been no report of the bioerosion of bird tissue (either fossil, archaeological, or modern). However, there have been several reports of bioerosion of other vertebrate tissues within the fossil record and it is pertinent to review these here.

The Bioerosion of Fossil Vertebrates

Wedl (1864) found tunnels in fossil reptile teeth and also in a variety of other material (bird egg shell, fish scales, corals and molluscs) from the Mesozoic to the Quaternary. He regarded the tunnels (with a diameter of

about 8μm) as being produced by fungi which grew at the expense of the host tissue by the absorption of the organic and inorganic phases of the bone. Wedl (1864) also experimented on the bioerosion of modern human teeth. Freshly extracted teeth were placed in untreated well water. After ten days branched tunnels were present in the cementum and dentine, although the enamel was unaffected. The diameter of the tunnels was about 8μm, the same as those present in the fossil material. This modern fungal bioerosion only penetrated 0.2-0.25 mm below the surface of the teeth and Wedl (1864) suggested that the ingestion of the organic and inorganic components together with the calcium salts of the teeth killed the fungi before any further penetration could take place.

Roux (1887) described similar bioerosion from Mesozoic and Quaternary reptile and fish bones and teeth. The tunnels were 2-12 μm in diameter. He named the trace *Mycelites ossifragus* (although he did not isolate or identify the organism). The tunnels (his term for them was 'Bohrkanäle') radiated from the Haversian canals into the osteon tissue.

Schaffer (1889, 1890, and 1895) examined Cretaceous reptile bones. These had been bioeroded and illustrated lamellate focal type of voids (see Figure 3.1). Although the morphology of the bioerosion patterns was different to that described by Wedl (1864) and Roux (1887), Schaffer described them as Roux canals (1890) and Wedl canals (1895).

Thomasset (1931) found tunnels in Carboniferous and Miocene fish teeth which he identified as *Mycelites ossifragus*.

Bystrov (1956) described bioerosion of the bones of ichthyosaurs and of the fish *Scaporhynchus* sp., *Holonema* sp., and *Rhytina* sp..

Marchiafava *et al.* (1974) studied the bioerosional activity of fungi of the genus *Mucor* in buried bone, and observed pits and tabular channels with well-defined walls. They placed pieces of sterilised human vertebrae in garden soil (at 20°C). A white mould covered the pieces after a few days; by the 45th day the cancellous bone was thoroughly penetrated by a luxuriant mycelium from which fungi of three genera were isolated. These genera were *Mucor*, *Cladosporium* and *Candida*. Inoculating further sterile bone with *Mucor* spp. produced tunnelling in 25-30 days. The *Mucor* hyphae filling the tunnels were 2-6 μm in diameter and resembled those illustrated by Wedl (1864).

Marchiafava *et al.* (1974, p. 207) stated that the bioerosion is the result of absorption by the fungal membrane in contact with the bone, and that the material that enters the fungus is in solution. Enzymes and other substances that attack bone are present inside and outside the fungal membrane and attack crystallites and organic matter simultaneously. It is likely that a

substance spreads freely into bone tissue inducing de-calcification of the matrix when hyphae show the effects of ageing, such as increased numbers and size of vacuoles and the accumulation of the various products of metabolism, i.e. fat droplets or pigment (Marchiafava *et al.*, 1974; p. 207). Marchiafava *et al.* (1974) stressed that in culture hyphae can only spread into fresh medium. The accumulation of products (of their own growth) changes the environment and slows down growth in an ageing colony. They examined Neanderthal (*Homo neanderthalensis*) bone material and found that tunnels occurring in it were narrower than those induced by *Mucor* in recent bone. The tunnels in the fossil material were 2-6 μm in size and this compares well with other documented fossil material (for example Wedl, 1864; Roux, 1887; and Schaffer, 1889, 1890, 1895). Scanning electron micrographs of the Neanderthal bone (Marchiafava *et al.*, 1974; p. 207) show that the walls of the tunnels are sharp and well calcified up to the free edge, and suggest that the tunnels of 2-4 μm may have been formed by the confluence of smaller ones 0.3-0.8 μm in diameter. The tunnels were irregularly interconnected to form a complicated labyrinth-like pattern.

Gouget and Locquin (1979) reported bioerosion in Devonian fish teeth and scales. The tunnels they described were 2-9 μm in size. They are restricted to the boundary between the dentine and enamel of the teeth. In some of the material the boring organisms are preserved and consist of fungal material (which they described as *Mycobystrovia lepidophaga*), and unnamed coccoid bacteria (Gouget and Locquin, 1979).

Hackett (1981) reported that a well-defined, simple and extensive branched tunnel (5 μm in size) was found in a Jurassic pterodactyl bone. No other information about this pterosaur bone was given in his report which extensively described bioerosion in exhumed human bones (see below).

Martill (1989) described the fungal bioerosion of neoselachian teeth from the Oxford Clay (Jurassic) of England. The tunnels described by Martill (1989) were 2-7 μm in size and were referred to as *Mycelites enameloides*. These tunnels were different to those described by Gouget and Locquin (1979) but were similar to those described by Bystrov (1956) and were remarkably similar to those described by Roux (1887). The tunnels, however, were limited to the enamel of the fossil teeth.

Martill (1991) figured the microbored surface (by fungi or ?bacteria) of a scale of the fish *Notelops* sp. from the Cretaceous Santana Formation of Brasil.

The Bioerosion of Archaeological Human Bones

Within the archaeological record there have been reports of the bioerosion of vertebrate tissue, but these studies have been restricted to human remains. Despite this, it is pertinent to review this research here as it provides descriptions of tunnel morphologies and also provides terminological schemes which can be followed.

Sognnaes (1955) studied microscopical changes in ancient (several centuries B.C.) and more recent human teeth. Three types of postmortem tunnels were found with diameters of 2-10 μm, 15-25 μm, and 50-100 μm. Sognnaes proposed that tunnels of different diameters resulted from differences in the types of tissues invaded, rather than by different organisms.

Morgenthaler and Baud (1956) described three conditions in human bones (from 12,000 years B.P. to the sixteenth century). In the first the microscopical structure of the bone was completely preserved, in the second it was preserved in parts, and in the third it was completely destroyed. They reported many minute canaliculi (they termed them 'canaux de forage') disrupting the structure of the bone which they thought to be the product of a micro-organism. However Hackett (1981) re-investigated the affected bones and revealed diagnostic characters (filaments, vegetative and fertile hyphae) of the soil fungal family *Dermatiaceae* in some of the osteon canals.

Werelds (1961, 1962 and 1967) reported more detail of postmortem tunnels in exhumed teeth from Belgium. Werelds (1961) described tunnels in teeth from 4th to 9th century burials in a sandy soil at Coxyde and from burials between 1235 and 1790 at Vivegnis (Werelds, 1962). The tunnels (his terms 'canaux', 'lacunes', 'galeries' and 'trous') in the tooth cement were straighter and thicker than those in the dentine, which he attributed to the differences between these tissues. The tunnels were always separated by wisps of unchanged cement or dentine and were between 5-20 μm wide. Werelds (1967) identified fungi with a "streaming-like" appearance in the tunnels of human teeth (presumably he was referring to a dendritic pattern). He also concluded that tunnels may appear sooner after burial than is generally expected.

Hackett (1981) surveyed the tunnelling (his term 'microscopic focal destruction') of exhumed human bones from a range of locations and ages. He noted that this bioerosion could be differentiated from the sequences of changes in pathological infiltration, new bone formation, and healing. He classified the types of tunnels into four readily recognisable forms; Wedl, Linear longitudinal, Budded and Lamellate (see Figure 3.1). He noted that Wedl tunnels were produced by *Mucor* species of fungus (Marchiafava *et al.*, 1974) and also *Fuscarium* sp. (Hackett, 1981). Early workers (e.g. Roux, 1887

etc.) had already deduced that such tunnels were produced by a fungus, and named it *Mycelites ossifragus*. More recently Martill (1989) described a second species *M. enameloides*. It is very likely that Wedl tunnels have more than one fungal originator, and for fossil Wedl tunnels (where it is impossible to identify the originating fungus) Martill's (1989) lead of using ichnogenus taxonomy should be followed.

Hackett (1981) further noted that one kind of tunnel morphology does not change into or overlap with another. He also reported that the inhumation environment of the bone influenced the presence of tunnelling. Burial in dry localities (for example dry rocky/limestone caves and stone sepulchres) prevented the occurrence of tunnelling. Wet or waterlogged conditions also prevented or retarded tunnelling (for example the wet soil of a London Cemetery). A soil with moderate soil moisture and periodical, seasonal variation of water table and temperature seemed to be most favourable for tunnelling.

Piepenbrink (1986) examined twenty exhumed bones from Switzerland and Germany covering inhumation periods from 200 to 1300 years ago. The bones were well preserved at the macroscopic scale. He observed natural staining of the bones (three colours were present; red, black and violet blue). These stained regions always showed microscopic decomposition of the bone. These decomposition patterns were subdivided into three categories: dissociation of the osteons, radial and tangential cracking of the hard tissue, and erosion of the cortical bone surface. He identified the following fungi as the cause of the bone destruction; *Stachybotrys cylindrospora*, *Doratomyces stemonitis*, *Pythium* sp., and *Rhizoctonia* sp. The tunnels that these fungi produced were 7 to 90μm in diameter. They were of the lamellate foci type (Piepenbrink, 1986; *sensu* Hackett, 1981). Piepenbrink (1986) further argued that the staining was produced by the acid metabolites from the saprophytic micro-organisms which invaded the bone post-mortem. From these observations he defined a model of biogenous decomposition of dead bone. Saprophytic micro-organisms grow superficially on dead bone and invade vascular channels. Excretion of enzymatic and/or acid metabolites follows, in order to utilise the energy content of the organic bone matrix. These metabolites diffuse more or less deeply into surrounding tissue and hydrolyse high molecular weight organic components. The products are used in the microbial metabolic processes. This selective loss of organic material causes cracks in the bone tissue resulting from shrinkage of the remaining substance. Brushite, $Ca(HPO_4).2H_2O$, formation by acid metabolites (upon the hydroxylapatite, $Ca_5(PO_4)_3(OH)$, component of the bone) leads to further structural

decomposition. In addition, the invading micro-organisms may excrete staining and fluorescing secondary metabolites that impregnate the bone tissue durably. As the staining of bone is accompanied by acidity (brushite formation) the most likely agents are fungi as they commonly prefer acid conditions and are able to adjust the pH to their requirements (Piepenbrink, 1986).

Garland (1988) examined the palaeohistology of human bones from a bone 'crypt' (ossuary) in the Parish Church of Rothwell, Northhamptonshire. He noted that destructive changes had occurred on a microscopic scale. These involved a general loss of micromorphology in the outer third of the cortex, predominantly affecting the outermost aspect of the osteons. Focal loss of collagen and mineral occurred and zones of hypermineralisation developed surrounding the foci (although Garland (1988) did not classify these focal destructive changes using Hackett's (1981) terminology these changes would be best described as "cuffing" *sensu* Hackett, 1981). Garland (1988) noted that loss of organic matrix was evident in the decalcified sections of bone as broken up Haversian systems. He also described inclusions characterised by fungi in the trabecular bone and within Haversian canals and by brushite crystals in association with cracks and fissures running through the bone microstructure. Garland (1988) identified and summarised six points in the taphonomic history of these bones. 1. There has been destruction and alteration of both the organic and inorganic components; 2. Slow post-mortem demineralisation of the bones is taking place and this mineral is being re-precipitated inside the bones, some in the form of brushite crystals. These crystals can be considered as space-occupying lesions, and are factors contributing to the cracking and fissuring of the histological morphology; 3. Loss of both organic and inorganic components has led to shrinkage and cracking of the bone microstructure; 4. Intrusive fungi are present inside the bones and they are accelerating the destructive processes; 5. At some stage in the history of the bone collection iron has infiltrated into the outer cortical surface of many of the specimens; 6. Histology has demonstrated a number of important implications for the conservation of both the crypt and the bones.

3c. Methods.

To examine the bioerosion of modern bird bones the experimental method described in Chapter 2b1 was followed. There were two differences from this previously described method and these are: 1. The specimens that were not skeletonised were largely ignored as no bioerosion had occurred to these specimens. 2. The skeletonised specimens were examined in detail for

bioerosion on any bones. Once the bioerosion had been detected the organism causing the bioerosion and also the amount of bioerosion was recorded. These specimens were photographed using a Pentax P30T with 100mm macro lens and also using a Leica Wild M10 microscope with Leica Wild MPS 48 and MPS52 photographic attachments. The specimens were also examined under a binocular microscope. 3. An S.E.M. investigation was undertaken of six samples removed from the bioeroded bones of specimens of a Ringed Turtle Dove (*Streptopelia risoria*), and a Double Crested Comorant (*Phalacrocorax auritus*).

Archaeological bird material from a Neolithic cave site (calcareous cave soils), Island of Gozo, Malta and a Roman midden (terrestrial rubbish pit), Bath, England were examined. The bones were examined by using non-destructive surface light microscopy. Where the bones were already broken this enabled examination of the internal areas. If bioerosion was present then the form, amount and locality of the bioerosion was recorded. Photographs were taken of bioeroded areas using a Leica Wild M10 microscope as above.

Fossil bird material from the Eocene (approximately 40 M.Y.A.) London Clay of S.E. England (in the collections of the Natural History Museum, London) was examined for evidence of bioerosion (see Table 3.3 for details). The specimens were only investigated by non-destructive light microscopy as this collection contains many holotypes and paratypes and destructive methods (thin section, S.E.M. etc.) could not be used. However, if the bones were already broken then internal examinations by the above methods were undertaken. If bioerosion was present then the form, amount and locality of the bioerosion was recorded.

3d. Results

3d1. Experimental Results

Sixteen specimens show evidence of bioerosion on some bones of the carcass (sample size, n=64 i.e. 25% of all specimens used). These are listed in Table 3.1.

The onset of bioerosion occurred rapidly. The earliest signs were evident within four days (specimen SSUP4, Northern Cardinal - *Richmondena cardinalis*). This specimen had signs of bioerosion on the skull (the frontal, squamosal and parietal bones). After 11 days all the other 15 specimens affected showed signs of bioerosion. This bioerosion was easily identified macroscopically as the bone was stained either green or blue-green in colour.

The organisms that produced the bioerosion within the specimens were section III and section V endolithic cyanobacteria (*sensu* Allaby, 1992) (Figures 3.2 and 3.3) and algae (Figures 3.4 and 3.5). The majority of endolithic cyanobacteria and algae are seen to enter the bone via pores within the outer lamellar cortical layer.

Some, however, remain on and colonise the outer surface of the bone and proceed to bioerode this outer periosteal surface, producing a meandering pattern of tunnels (Figure 3.6).

The majority of endolithic cyanobacteria and algae that enter the bone rapidly colonise the trabeculae of the cancellous zone (Figure 3.7). Under magnification these organisms can be seen to have repeatedly bored into the trabeculae creating tunnels (Figures 3.8). These tunnels are of the Wedl type (*sensu* Hackett, 1981) (compare Figure 3.8 with Figure 3.1). This weakening of the fabric of the bone eventually causes disintegration (Figures 3.9 and 3.10). Disintegration occurs first in the naturally thin areas (e.g. the sternal plate area: Figure 3.11) and proceeds to thicker areas of the bone, e.g. the carina area of the sternum (Figure 3.10). The process continues until the bone completely disintegrates.

Extensive bioerosion damage tended to occur in those bird bones that have naturally thin outer lamellar cortical layers and are comprised mainly of cancellous bone. These bones are those usually not strengthened for use in flight or walking (i.e. those bones which are generally reduced in weight to aid flight). This correlation can be seen in Table 3.2.

Light was observed to play an important part in colonisation by bioeroders. For example a skull of a Double Crested Cormorant (*Phalacrocorax auritus*) was partially buried in sediment. The area protruding from the sediment was colonised by algae and endolithic cyanobacteria but the portion that was buried had no colonisation. It was also observed that bones which contained large amounts of fat ('marrow') were more resistant to bioerosion. The bioeroders may not have been able to tolerate the organic compounds, or the fat may have extruded and blocked any pores/entrances, thus preventing the entry of bioeroders.

3d2. Archaeological Material

Examination of the archaeological bird material from a Palaeolithic cave site (dry calcareous cave soils), Malta and a Roman midden, Bath, England revealed evidence of bioerosion. Four bones (1 left carpometacarpus, 1 right coracoid, 1 left ulna, 1 left humerus) from the Palaeolithic site were bioeroded (sample size = 4, i.e. 100% of the sample). The bioerosion consists of isolated tunnels and branching meandering

tunnels upon the periosteal surface of the bone (Figure 3.12). The tunnels are approximately 0.25mm in width, although this width is variable along the length of the tunnels. The tunnels do not appear to penetrate further than approximately 0.2mm into the outer lamellar cortical layers. Extensive damage (destruction of the outer lamellar cortical layers) is limited to the thin areas of the bone. This is particularly evident upon the coracoid (the articular surface with the sternum, the *facies articularis sternalis*) where the outer lamellar cortical layer is destroyed revealing, the trabeculae of the cancellous zone.

The material (1 furcula, 1 right ulna, 1 right humerus, 1 vertebral portion of a synsacrum) from the Roman midden shows a form of bioerosion that does not make visible surface tunnels. The bioerosion is made evident from tracts of bone that are discoloured (Figure 3.13) (and also intermittent brushite formation, Figure 3.14). These tracts are approximately 0.2mm in width (although this is variable along their length). The discolouration is rusty brown and probably represents the oxidation of a secondary iron mineral deposited on the internal tunnels. These internal discoloured tunnels can be identified in broken surfaces of other bones (sheep - *Ovis sp.* and pig - *Sus scrofa*) in this deposit. In these mammalian bones the tunnels are discrete, small (approx. 0.25mm), branching, meandering traces which occur in the lamellar cortical bone adjacent to the endiosteal surface. Piepenbrink (1986) recorded staining of human bones and brushite formation (see above) which were caused by the metabolic activities of bone decomposing fungi.

3d3. Palaeontological Material

Examination of 13 specimens from the Eocene (approx. 40 M.Y.A.), London Clay (various localities in S.E. England) produced evidence of bioerosion of bird bones in the fossil record (Table 3.3). In 77% (10 specimens, n=13) of the specimens examined bioerosion of the outer periosteal surface had occurred. The bioerosion consists of meandering surface tunnels which are approximately 0.25mm in width, although this width is variable along the length of the tunnels. The tunnels do not appear to penetrate further than approximately 0.2mm into the outer lamellar cortical layers. This bioerosion was not seen to cause extensive damage and in the thirteen specimens the bioerosion was localised to small discrete areas.

3e. Discussion

It is apparent that bioerosion only occurred in 25% (n=64) of the modern bones. The lack of bioerosion within the other 75% of specimens can be explained by one of the following factors:

1. The rapid burial of the specimens under sediment. Therefore preventing any organism attacking the bone (this occurred in 5 specimens i.e. 8% of the total sample, n=64).
2. Decay had not proceeded for long enough to allow the exposure of skeletal elements. Therefore the bones were not exposed to any bioeroding organism (this occurred in 17 specimens i.e. 27% of the total sample).
3. The specimen was totally removed from the site by the action of scavengers. Therefore the bones and specimen were destroyed (this occurred in 25 specimens i.e. 39% of the total sample, n=64).

Therefore only 1% (n=64) of the specimens were not bioeroded (of those that were not excluded by one of the above factors) i.e in most of the specimens where bioerosion could occur it did occur. This therefore indicates that bioerosion may play an important role in destroying bone and creating information loss to the fossil record. The speed and large scale amount of bioerosion observed indicates that these processes are, taphonomically, very important as a destructive agent of bone in shallow marine/freshwater environments where bone is expected to be well preserved.

The meandering pattern of surface tunnels seen in the modern, archaeological and palaeontological specimens are very similar to Wedl tunnels, although Hackett's (1981) classification strictly describes Wedl tunnels as those within the vertebrate tissue which pass away from the surfaces of the cortex and the osteon canals (i.e. generally perpendicular to the periosteal surface) (see Figure 3.1). As these tunnels are generally parallel to the periosteal surface I propose that they are termed Hackett tunnels (in honour of the pioneering work upon this subject by the late Dr. Cyril J. Hackett). Upon comparison of these Hackett tunnels with *Mycelites enameloides* (Martill, 1989) it can be seen that they are very similar. It is likely therefore that the ichnogenus *Mycelites* is also caused by cyanobacteria/algae which attack compact vertebrate tissues such as the enamel of teeth and the periosteal surface of lamellar cortical bone.

Endolithic cyanobacteria and algae are influenced by environmental factors such as sunlight, current strength, temperature and salinity. These factors may all be controlled by water depth (Swinchatt, 1969; Golubic et al., 1975; Akpan, 1986 and 1990). Although these organisms have a worldwide distribution they have their highest frequency in low energy, tropical, shallow marine environments (Hessland, 1949). This type of environment would be expected to preserve vertebrate material quite well but the action of bioerosional activity of organisms would create effects that would simulate

transport and mechanical abrasion (compare Figure 3.10 with Figure 4.8, Chapter 4). This would also result in a loss of information from the fossil record in any environment in which bioerosion could occur. The amount of information loss would be difficult to ascertain, but it can be assumed from this preliminary experiment and observation of archaeological and palaeontological material that this information loss is higher than previously expected.

The archaeological material showed evidence of two types of bioerosion and one other type of bone destruction (brushite formation). The bioerosion types were Hackett Tunnels and tunnels with fungal staining. This is consistent with the results of the modern experiments and shows that bioerosion can be arrested. The bioerosion of the Palaeolithic cave material is likely to have been fungal as opposed to algal or endolithic cyanobacteria since, as mentioned previously, the latter requires light and water to be present. The production of Hackett Tunnels by ?fungal originators shows that tunnel morphology is not indicative of the causational organism and hence caution must be employed when speculating about the identity of bioeroding organisms. The Roman midden material also indicates that bioerosion can be halted by exclusion of light (specimens from deeper in the midden are bioeroded less i.e. exclusion of light due to burial under further rubbish) or by a change to hostile environmental conditions (the lower portions of the midden were extremely hostile as indicated by brushite formation (indicating highly acidic conditions) and also the formation of pyrite and their precursors (as can be seen on the bone surfaces and within medullary cavities) indicating reducing, anoxic conditions.

The palaeontological material shows evidence of Hackett tunnels. This indicates that bioerosional activity has been present within the geological past. It becomes more difficult to speculate on the causational organisms of this bioerosion because it is not evident whether this bioerosion was caused on land (and then the bones were transported to be deposited within the marine sediments of the London Clay) or whether the bioerosion occurred in these marine conditions. The tunnel morphology does not give any further evidence to solve this problem. It is likely, however, that bioerosion was occurring with the sub-tropical, shallow marine conditions of the London Clay environment as these conditions are ideal for bioeroders (see Hessland, 1949).

3f. Conclusions

1. This study produces the first evidence of bird bone bioeroders in modern, archaeological and palaeontological situations.

2. It indicates that endolithic cyanobacteria and algae are responsible for large scale destruction of bone in certain environments.

3. From the archaeological evidence this destruction of bone occurs in other environments such as cave deposits and middens.

4. Bone that appears at the macroscopic level to be well preserved, in fact, can have large amounts of microscopic fabric destruction.

5. The rate and speed of bioerosion is much faster than previously recognised, although this is controlled by environmental factors such as temperature, water depth, sunlight, current strength and salinity.

6. Bioerosional activity can mimic the effects of mechanical transport. This must lead to careful taphonomic analysis before transport is cited as the cause of bone destruction.

7. Bioerosion creates information loss. This cause of information loss from the geological record is higher than previously expected and can cause information loss in environments where preservation is expected to be good.

8. The exact amount of information loss due to bioerosion is unknown. The rates of bioerosion in differing environments is also unknown. These therefore require further assessment to aid in taphonomic studies.

DAY	FLUP	FLP	SLUP	SLP	FSUP	FSP	SSUP	SSP
1	¥	¥	¥	¥	¥	¥	¥	¥
4	¥	¥	Rem.	¥	¥	¥	Bio.	¥
7	¥	Bio.	Rem.	¥	¥	Not.	Rem.	†
11	Bio.	†	Rem.	Rem.	Bio.	Bio.	Rem.	†
28	Bio.	Bio.	Bio.	Bio.	Rem.	Bio.	Rem.	Bio.
56	Bio.	Bio.	Bio.	Bio.	Rem.	Rem.	Rem.	†
70	Bio.	Rem.	Rem.	Rem.	Rem.	Rem.	Rem.	†

Table 3.1. Categories of experimental specimens indicating those that have bioeroded bones. Each box represents one carcass

¥ = Specimen not skeletonised

† = Specimen rapidly buried under sediment

Bio. = Bones Bioeroded

Rem. = Specimen removed by scavengers

Not. = No bioerosion

Skeletal Element	Total Number of Bioeroded Bones	Corrected Total (see legend below)	List of most commonly bioeroded skeletal elements based on the corrected total.
Skull	12	12	1. Synsacrum
Mandible	10	10	2. Sternum
Vertebrae	10	0.38	2. Skull
Ribs	8	0.57	4. Mandible
Sternum	12	12	5. Furcula
Furcula	9	9	6. Ulna
Scapulae	7	3.5	6. Humerus
Coracoids	9	4.5	8. Femur
Humeri	10	5	8. Tibiotarsus
Radii	8	4	8. Coracoid
Ulnae	10	5	11. Radius
Carpometacarpi	7	3.5	11. Tarsometatarsus
Wing digits	8	0.8	13. Scapula
Synsacrum	13	13	13. Carpometacarpus
Femora	9	4.5	15. Wing digits
Tibiotarsi	9	4.5	16. Ribs
Tarsometatarsi	8	4	17. Pes digits
Pes digits	7	0.5	18. Vertebrae

Table 3.2. Numbers of bioeroded skeletal elements and list of skeletal elements showing "bioerodability". Elements that are mainly comprised of thin lamellar cortical bone are more likely to be bioeroded e.g. Sternum, skull, mandible etc. This can be correlated with structural integrity of the bone.
Corrected total (Minimum Number of Individuals, MNI) calculated by dividing the total number of skeletal elements bioeroded by the number of skeletal elements in a skeleton (e.g. 10 bioeroded humeri divided by 2 (2 humeri in each skeleton) = a corrected total of 5).

Name	Catalogue Number	Description of Specimen	Description of Bioerosion
Precursor parvus	BMNH A3684	Distal end of left humerus	Hackett type tunnels in the brachial depression of the humerus
Precursor parvus	BMNH A3553	Proximal end of left humerus	Hackett type tunnels on the bicipital surface
Precursor litorum	BMNH A3135	Distal end of right humerus	Hackett type tunnels on the ridge between the internal and external tricipital grooves
Precursor magnus	BMNH A4356	Proximal end of left carpo-metacarpus	Hackett type tunnels in the tendinal groove on metacarpal II
Precursor magnus	BMNH A3683	Distal end of right tarsometatarsus	Hackett type tunnels in the outer extensor groove
Promusophaga sp.	BMNH A43165	Proximal end of left femur	Hackett type tunnels on the sinistral side of the trochanteric ridge
Promusophaga magnifica	BMNH A33138	Proximal end of left humerus	Hackett type tunnels on all parts of the specimen
Promusophaga magnifica	BMNH A38935	Sternal plate area of sternum	Hackett type tunnels on the sternal plate
Promusophaga magnifica	BMNH A38934	Proximal end of right humerus	Hackett type tunnels on all parts of the specimen
Parvicuculid	BMNH A5291	Distal end of left humerus	Hackett type tunnels on all parts of the specimen
Primapus lacki	BMNH A2166	Complete left humerus	Hackett type tunnels on all parts of the specimen

Table 3.3. Bird specimens in the collections of the Natural History Museum, London, from the Eocene London Clay of S.E. England showing evidence of bioerosion.

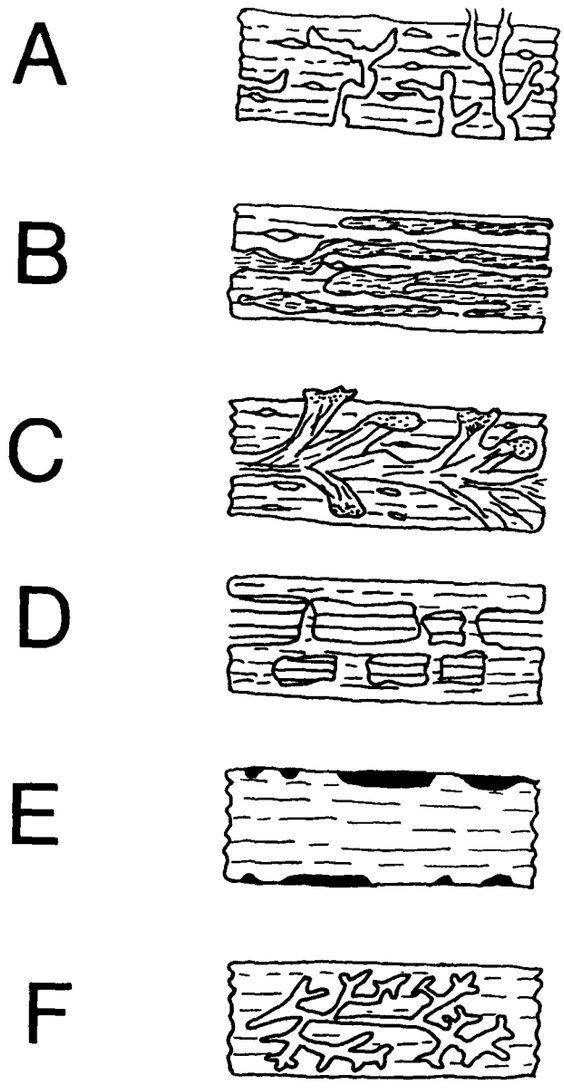


Figure 3.1. The five types of tunnels/foci made by bone bioeroding organisms.

A = Wedl Tunnels (view in cross section)

B = Linear Longitudinal Tunnels (view in cross section)

C = Budded Tunnels (view in cross section)

D = Lamellate Tunnels (view in cross section)

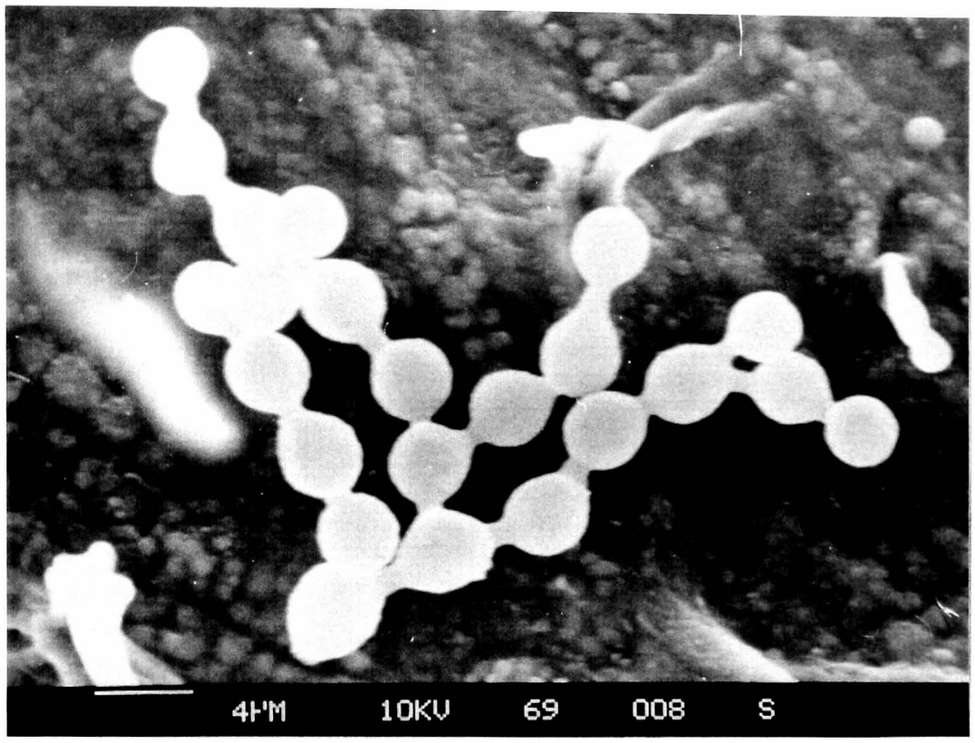
E = Hackett Tunnels (view in cross section)

F = Hackett Tunnels (plan view i.e. periosteal surface view)

Figures A to D redrawn from Hackett (1981).

Figure 3.2 Section III cyanobacteria found bioeroding the endiosteal surface of the sternum of a Ringed Turtle Dove (*Streptopelia risoria*) (SSP 28).

Figure 3.3 Section V cyanobacteria found bioeroding the endiosteal surface of the sternum of a Ringed Turtle Dove (*Streptopelia risoria*) (SSP 28). The tunnel produced is approximately 4 microns wide.


4µM 10KV 69 008 S

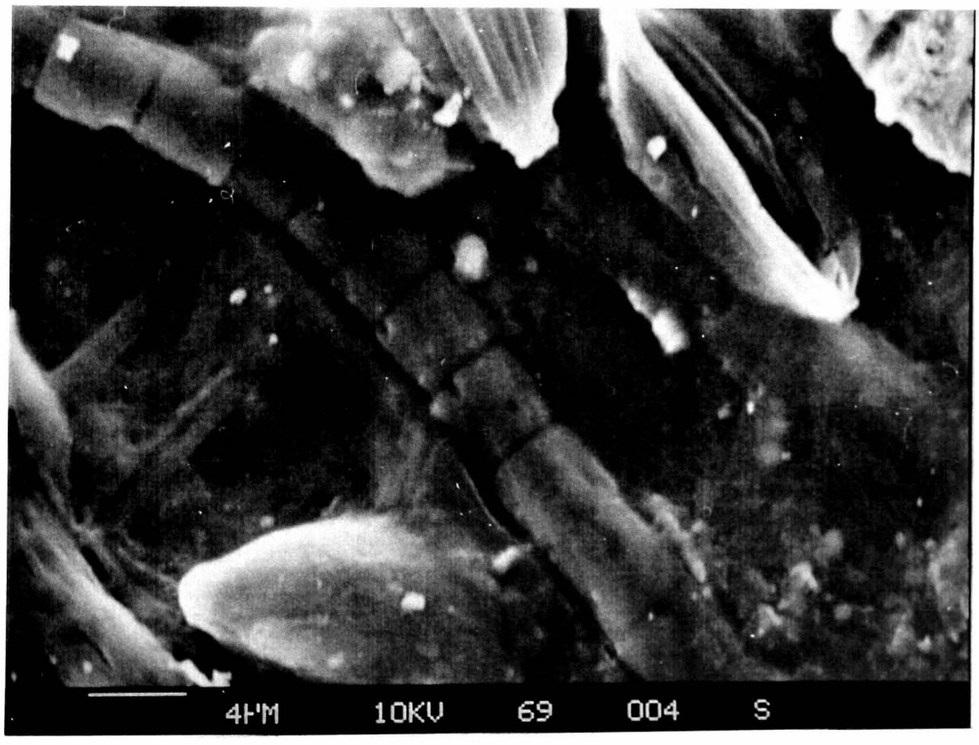

4µM 10KV 69 004 S

Figure 3.4 Algal filaments bioeroding the outer (periosteal) surface of a Double Crested Cormorant (*Phalacrocorax auritus*) humerus (SLP 56). Magnification = x11.

Figure 3.5 Algal filaments (arrowed) bioeroding the endiosteal surface of the sternum of a Ringed Turtle Dove (*Streptopelia risoria*) (SSP 28).

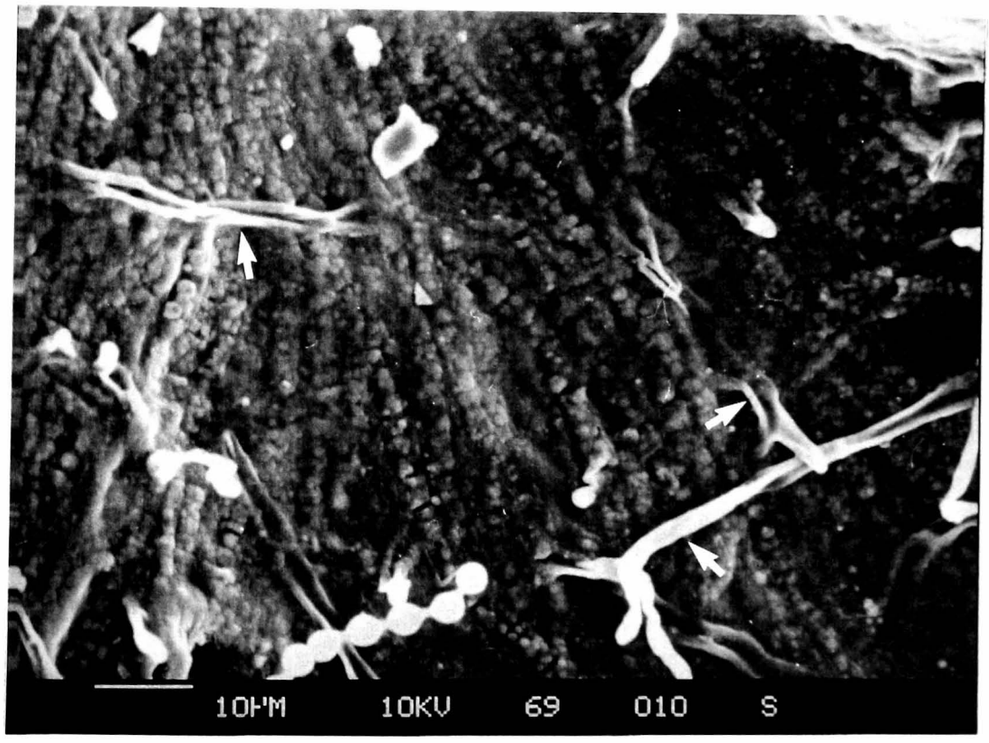
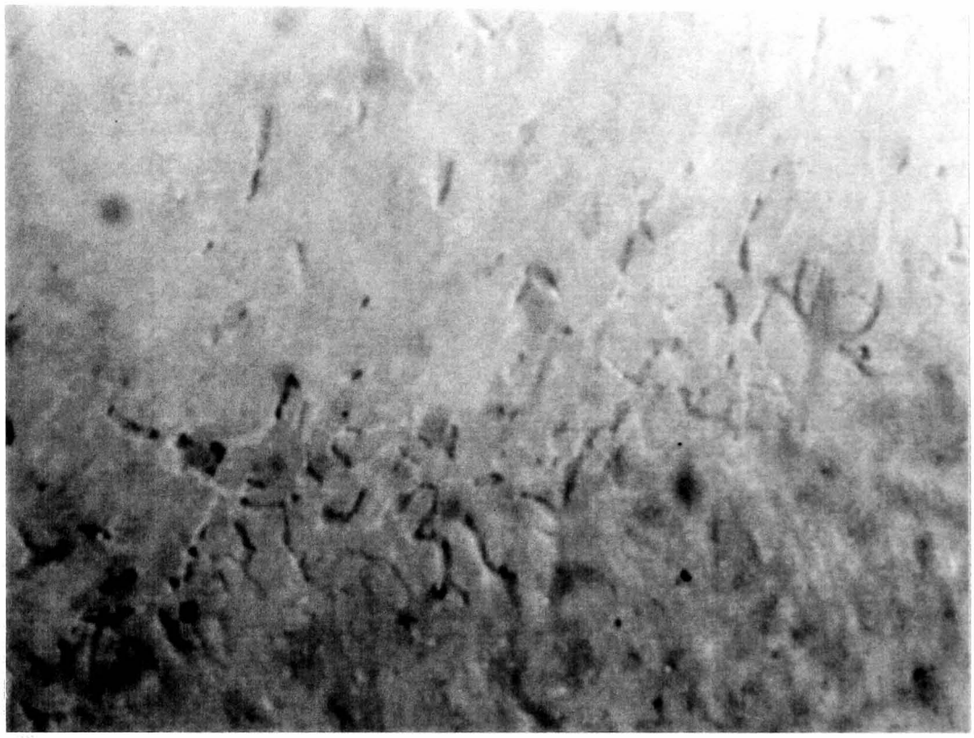

10μM 10KV 69 010 S

Figure 3.6 Meandering pattern of Hackett tunnels on the periosteal surface of a Double Crested Cormorant (*Phalacrocorax auritus*) sternum (SLP 56). The tunnels are approximately 4 microns in width. Magnification = x38.



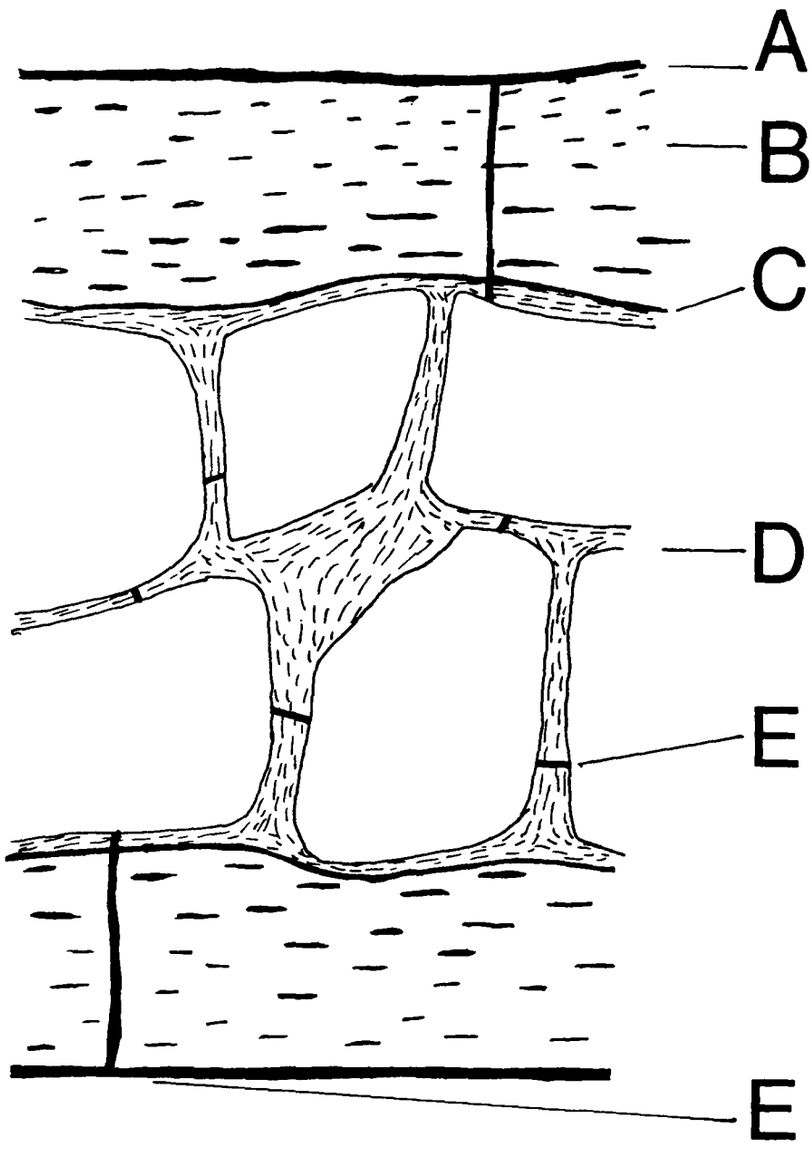


Figure 3.7. Schematic cross section through a bird bone. x200

A = Periosteal surface

B = Lamellar Cortical Layer

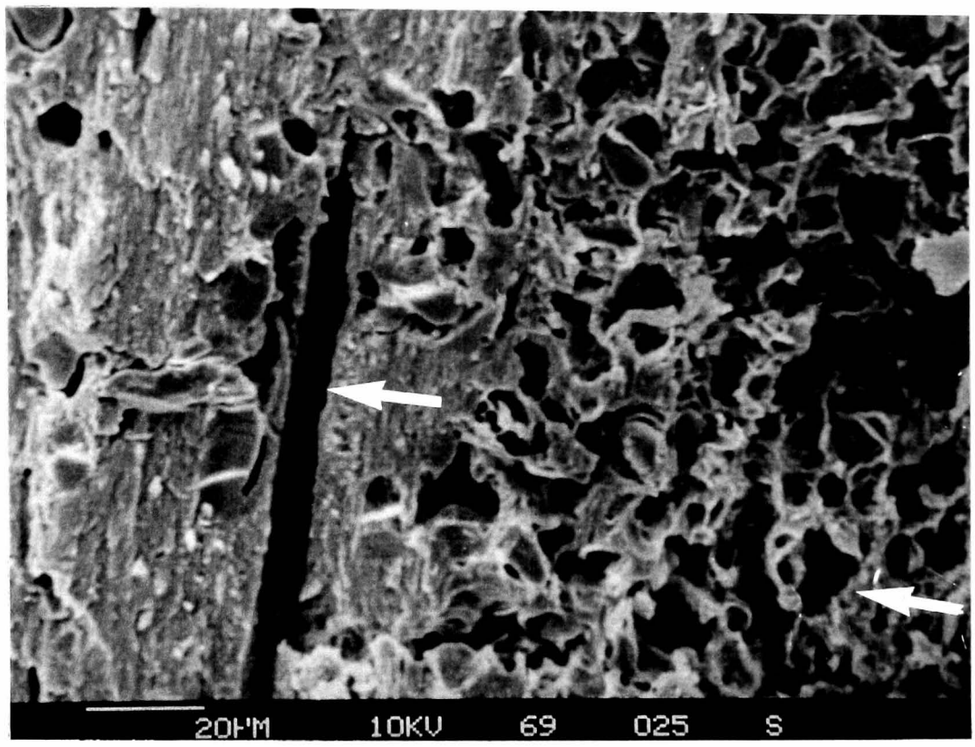
C = Endosteal surface

D = Trabecular Layer

E = Pores / pneumatic openings / blood vessel openings

Figure 3.8 Large scale destruction of the outer lamellar cortical layer of a Double Crested Cormorant (*Phalacrocorax auritus*) humerus (SLP 56). The lamellar cortical bone nearer the periosteal surface is worse affected (far right arrow). A discrete Hackett tunnel (left arrow) can be seen running perpendicular to the periosteal surface. This tunnel is approximately 5 microns in diameter.

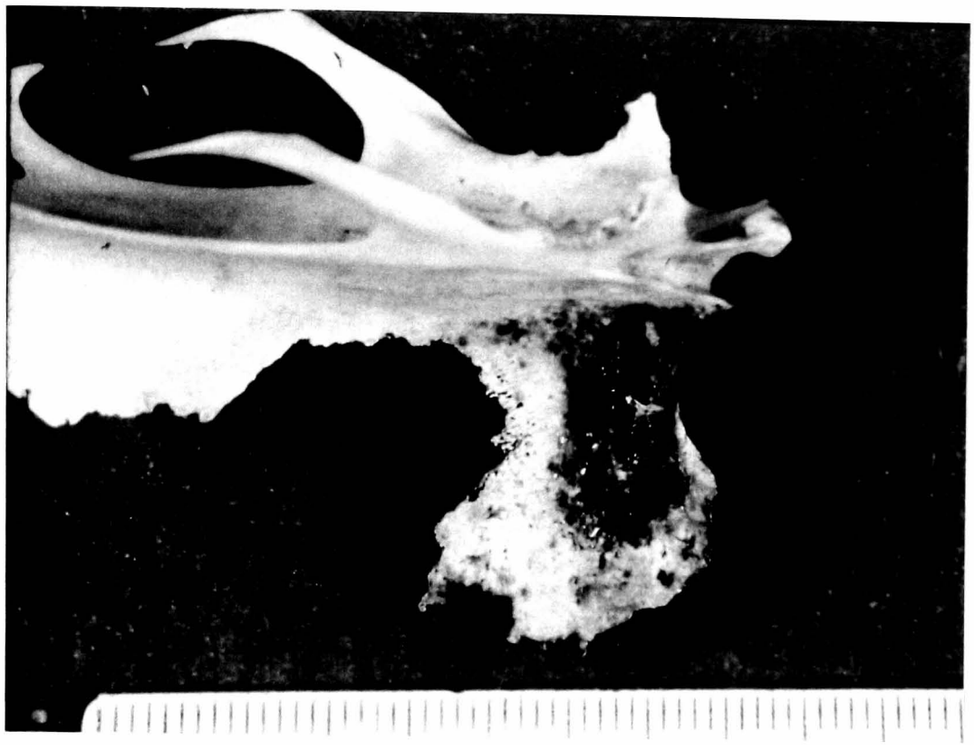
Figure 3.9 Destruction of bone caused by extensive bioerosion. The front portion of the skull (Ringed Turtle Dove, *Streptopelia risoria*, SSP 28) has been totally removed.


20µM
10KV
69
025
S


METRIC
2
3
4
5

Figure 3.10 Heavily bioeroded sternum of a Ringed Turtle Dove (*Streptopelia risoria*) (SSP 28). The pattern of bone loss can be compared with that caused by abrasion (see Figure 4.8).

Figure 3.11 Bioeroded sternum of a Double Crested Cormorant (*Phalacrocorax auritus*) (SLP 56). Bone loss has started to occur in the thin bone of the sternal plate region. This then proceeds to the thicker areas of bone e.g. the carina area of the sternum (see Figure 3.10).



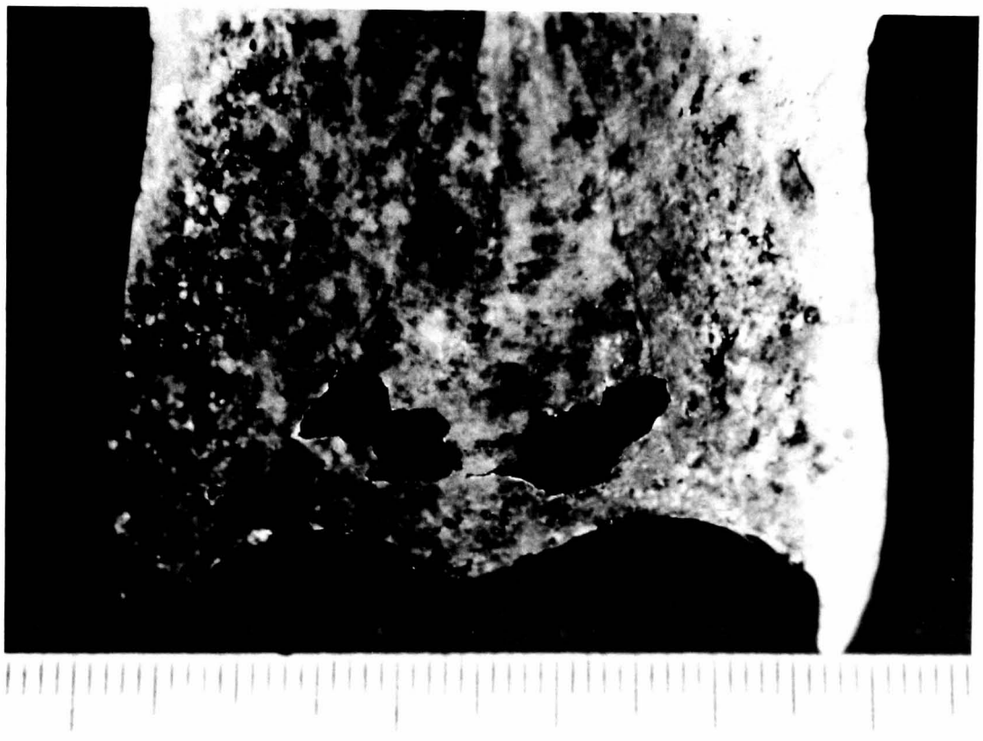


Figure 3.12 Branching, meandering Hackett tunnels on the periosteal surface of a bird ulna from a Palaeolithic cave site (Malta). The tunnels are approximately 20 microns in width. Magnification = x17.

Figure 3.13 Tracts of discoloured bone on a ulna from a Roman midden (Bath, England). The tracts indicate the prescence of bioerosion. The dicolouration is due to mineral precipitation. The tracts are approximately 15 microns wide. Magnification = x76.

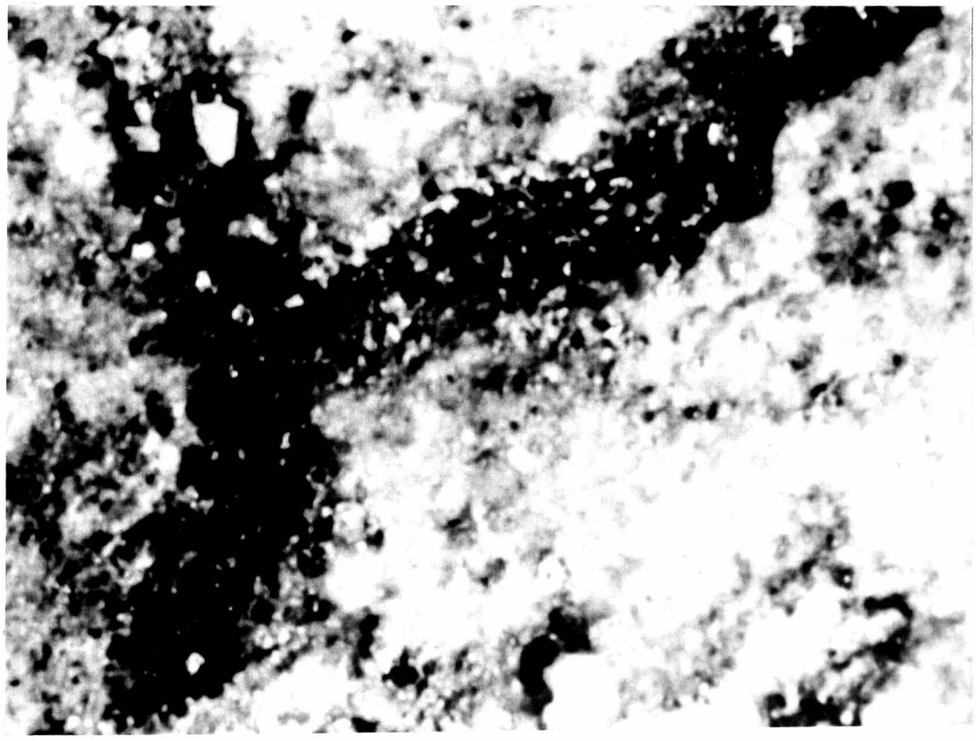
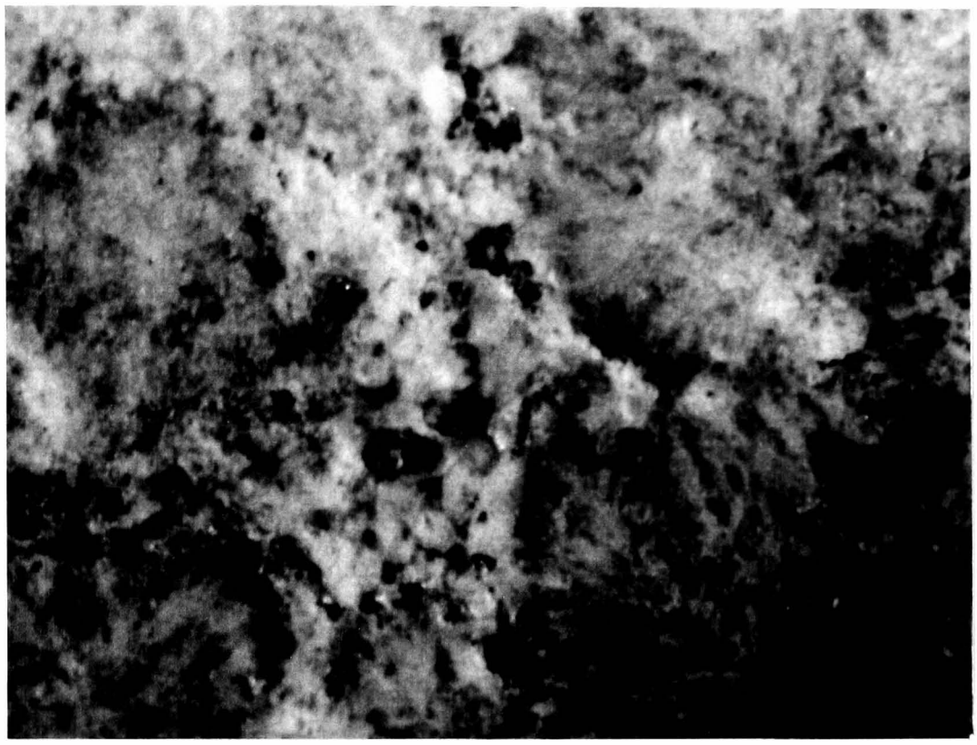


Figure 3.14 **A bird synsacrum from a Roman midden (Bath, England) showing the formation of brushite (bottom right of photograph). The texture of brushite is distinct and because it is less compact than unaltered bone it is preferentially destroyed.**



Chapter Four
Observational Taphonomy

4a. Introduction

Schäfer (1962) coined the term Aktuo-Paläontologie for the study of dead and decaying animals in the natural environment and its use as a basis for interpreting the fossil record. I prefer the term Observational Taphonomy for this type of study and it is used here in preference to Schäfer's terminology.

Observational taphonomy identifies the types of processes that affect birds in the natural environment, so that the factors controlling these processes can be investigated. The field data provided by observations are important because they provide a ground truth for experiments. They can confirm that conclusions based on somewhat artificial controlled experiments can be extrapolated to the natural environment.

4b. Bird Mortality

Dead birds can be observed in any environment and mortalities are usually due to the following factors, identified (originally in mammals) by Shipman (1981): predation, disease, senility (old age), accident and starvation/dehydration.

The death rate is greatest in juvenile specimens as they are more vulnerable to external factors, i.e. they are not independant, and rely on their parents for food, warmth and protection from predators. It has been estimated that 80% to 95% of juvenile birds die within their first year (Perrins, 1987) (Figure 4.1).

A table of adult annual mortalities of some British species of bird (Table 4.1) shows that the smaller species (body weight) have a higher than mean annual adult mortality and lower mean life expectancy. This is due to several factors:-

4b1. Predation

Predators prefer small prey, as they do not usually have the ability to "damage" the predator during the struggle and so are easier to catch. In addition, a small bird is vulnerable even to small predators, e.g. a sparrowhawk (*Accipiter nisus*) will catch birds nearly its own size e.g. woodpigeons (*Columba palumbus*) (pers. obs.).

4b2. Metabolism

All birds breathe about the same number of times during their lives and have about the same number of heart beats (Welty and Baptista, 1988). Thus they live the same amount of "relative time" even though the metabolism is higher and the heart beats at a faster rate in smaller birds and they die earlier (Welty and Baptista, 1988).

4b3. External factors

Small birds are more prone to the influence of external factors, such as temperature, food supply, water supply and habitat. This is because small birds live on a "knife edge" balance of their energy budget. For example a severe spell of weather can kill birds because the greater loss of heat from the body cannot be replaced quickly enough (Schäfer, 1972, reported upon many mass deaths caused by severe weather e.g. coots (*Fulica atra*) and starlings (*Sturnus vulgaris*) at Jade Bay in Heligoland).

Shipman's (1981) factors for the cause of death (predation, disease, senility, accident, starvation/dehydration), although originally identified in mammals, also apply to birds.

Predation

Both mammals and birds predate avian specimens. For example red foxes (*Vulpes vulpes*) prey on many species of birds, including pheasants (*Phasianus colchicus*) and woodpigeons (*Columba palumbus*) (pers. obs., Welty and Baptista, 1988, p. 388-391, give a comprehensive list of mammalian predators). Avian predators such as sparrowhawks (*Accipiter nisus*) and peregrine falcons (*Falco peregrinus*) will attack birds ranging in size from blue tits (*Parus caeruleus*) to red grouse (*Lagopus lagopus*) (pers. obs., Welty and Baptista, 1988, p. 388-391, give a comprehensive list of avian predators). Birds that have been killed by predators are rarely incorporated into the fossil record. This is because predators usually totally consume any kills that they make e.g., red fox (*Vulpes vulpes*) completely consumes a carcass only leaving a few feathers (pers. obs.) of mallard (*Anas platyrhynchus*) or woodpigeon (*Columba palumbus*). Avian predators, however, regurgitate any inedible portion of a carcass that they ingest and these "pellets" can form important bone accumulations below roost sites (Andrews, 1990, extensively documented the taphonomic implications of avian "pellets" in fossil cave deposits).

Disease

Diseases of birds fall into seven categories (Coles, 1985): bacterial, viral/rickettsial, mycotic, protozoal parasites, arthropod ectoparasites, helminth parasites, and poisons. These seven categories include a total of 89 possible causes of death (Coles, 1985). It is usually impossible to observe death of birds by disease as the symptoms cannot usually be observed. However I have observed a Blackbird (*Turdus merula*) dying of 'gapes' (syngamiasis), a helminth parasite, the symptoms of which are gasping for breath and shaking of the head. The parasites block the trachea which eventually causes death. This parasite is very common in Passeriformes and is passed by direct transmission or through a host such as earthworms, slugs and snails. Death by disease is impossible to observe within the fossil record as the causes of diseases do not preserve.

Senility

Senility (or old age) deaths are probably rare in wild bird populations. It is more likely that aged individuals will die of disease, predation or accident (Shipman, 1981). It is possible to assume that a bird has died of "senility" if the fossil bird contains exceptionally worn joint symphases (although caution must be used as certain diseases will create the same effect, e.g. osteoporosis (Coles, 1985). However, of all the fossil bird specimens that I have observed none had any pathological deformities.

Accident

Accidents are very common in the wild and are a major cause of bird deaths. Although accidents caused by fighting or flying into objects rarely cause death instantaneously, the injuries sustained will hasten death by any other of the mortality factors. I have observed male chaffinches (*Fringilla coelebs*) fighting over territory which caused wing injuries to one of the birds. These injuries were not immediately life threatening but left the bird unable to fly and very vulnerable to predators. Accident also includes catastrophic events e.g. debris flows, ash falls, flooding, drowning. Within the fossil record there is one very good example of avian death by accident. The Green River Formation of Lake Uinta (Chapter 5.3) contains a mass mortality horizon of *Presbyornis* bones. This horizon contains many thousands of bones of both adult and very immature individuals and I interpret this as a nesting colony. The bones are all resting on a eroded palaeo-land surface. Covering the bones is a horizon of tuffaceous composition (pers. obs.). I interpet this evidence as the catastrophic mass mortality of a nesting site of *Presbyornis* by the eruption of a nearby volcano. The volcano would have rained ash and

poisonous gases over the area so "instantaneously" killing both adult and juvenile specimens. The tuffaceous deposit overlying the bones is interpreted as debris flow which was propagated by the eruption. The bones within the deposit are always disarticulated and show signs of abrasion. It is envisaged that the debris flow swept along the palaeo-land surface and picked up the *Presbyornis* cadavers, disarticulating and abrading them.

Starvation/dehydration

The absence of the vital elements of food and water obviously cause bird mortality. Several factors may result in a shortage of food/water, and these are usually environmental or reflect population numbers.

Environmental factors such as severe winter weather, where all water sources have frozen and food sources are scarce, causes death. I observed this, during the severe winter of 1981, when mass mortalities of birds were recorded. Schäfer (1972) reported similar occurrences from a wide variety of sources.

The other cause of a lack of food/water results from variation in bird population numbers. Most ecosystems have a maximum "carrying capacity" for species. If the population exceeds carrying capacity then shortages occur. One of the natural responses to this is mortality (especially in the old, young and injured) to bring population numbers below the carrying capacity of the ecosystem (Welty and Baptista, 1988).

For the taphonomist examining the fossil record it is usually impossible to deduce any of these causes of death. It is only in rare occasions such as the accidental trapping of birds in asphalt at Rancho La Brea (Sutcliffe, 1986, Chapter 6f) or the *Presbyornis* mass mortality horizon, that cause of death can be inferred.

4c The decay of birds

The experiments described in Chapter 2 were in part observational, in that they were carried out in the natural environment with scavenging being controlled.

It is rare for anyone carrying out observational taphonomy to be present at the moment of death, therefore making it difficult to record the exact time when decay commences. Schäfer (1972) produced a "timed" disarticulation scheme for birds in the open ocean (Chapter 1) but this must be a minimum time as the bird may have died several days before the carcass was observed. By using the data obtained in the experiments of Chapter 2 it is possible to estimate the duration of decay based on the state of the carcass.

The decay of birds can be observed in the natural environment and there are a number of processes/animals that affect its progress.

4c1. Scavengers

Scavengers have an obvious effect on the decay of birds in that they eat soft tissues (and affect the rate of disarticulation, see Chapter 2). There are a variety of scavengers, including mammals, reptiles, fishes, birds, insects, crustaceans and molluscs.

Mammals.

I have observed red foxes (*Vulpes vulpes*), badgers (*Meles meles*), racoons (*Procyon lotor*), stoats (*Mustela erminea*), weasels (*Mustela rivalis*), European mink (*Mustela lutreola*) and otters (*Lutra lutra*) feeding on dead birds. Much of this observation is not direct i.e. watching them eat a bird, but is inferred from how the soft tissues have been eaten, the presence of droppings and from pawprints around the remaining carcasses.

Reptiles.

Chapter 2 mentioned scavenging by reptiles, in particular alligators (*Alligator mississippiensis*) and crocodiles (*Crocodilus americanus*). These reptiles eat cadavers whole, eliminating any possibility of their becoming fossilised. Other reptile scavengers are rare as most of those that eat birds (eg. snakes) are actually bird predators and do not scavenge carcasses.

Fishes.

If the cadaver is in the aquatic environment it will exclude many scavengers but it will suffer from scavenging by fish. Although I have only seen small fish scavenging the carcasses in the experiments that I conducted (Chapter 2), many fish will utilise a carcass as a food source. Possibly the most famous fish scavengers are the Piranha family. These fishes rapidly strip carcasses in the freshwater river systems of South America (and can devour large mammals in a matter of minutes, Dempsey, 1984). Most importantly, even though they are most voracious, they do not damage the skeleton, which remains intact. This is true for most scavenging fish as they only pull small mouthfuls of soft tissue off at any one time. Therefore fish allow the skeleton to remain intact with the possibilty of being fossilised (unlike many other scavengers).

Birds.

Birds themselves scavenge bird carcasses. Apart from the turkey vultures (*Cathartes aura*) mentioned in Chapter 2, I have observed buzzards

(*Buteo buteo*), kestrels (*Falco tinnunculus*), carrion crows (*Corvus corone*), rooks (*Corvus frugilegus*), jackdaws (*Corvus monedula*), magpies (*Pica pica*), herring/lesser black backed/greater black backed/black headed gulls (*Larus argentatus, fuscus, marinus, ridibundus*) and green woodpeckers (*Picus viridis*) all feeding on avian carrion. The pellets these birds produce can be taphonomically important in the accumulation of deposits of bird bones (see Andrews, 1990).

Insects.

Many insects scavenge bird carcasses. If they do not eat the carcass directly many lay eggs in the cadaver which then provides food for their developing larvae. Figure 4.2 shows a woodpigeon (*Columba palumbus*) that has been killed and half eaten by a domestic cat (*Felis domesticus*). The open flesh was covered with blow flies (*Calliphoridae* family) laying eggs and feeding. Blow fly eggs hatch into larvae which are more commonly known as maggots. Maggots rapidly consume a carcass and also increase the temperature of a cadaver to up to 50^{o}C (pers. obs.). This increase in temperature also allows bacteria to grow at maximum rates which quickly consume any soft tissues. As well as the blow flies, wasps (*Vespula* sp.) were feeding on the soft tissues.

Other insect scavengers I have observed include burying beetles (*Nicrophorus humator* and *littoralis*), and ants (*Formica* spp.) within a black headed gull (*Larus ridibundus*) carcass, and giant water scavenging beetle (*Hydrophilus triangularis*) (see Chapter 2).

Crustaceans.

Many crustaceans are scavengers. In the freshwater environment of the experiments (Chapter 2) crayfish species (including *Procambarus gracilis*) were observed eating the carcasses of birds. At the locality of the seawater experiments (Figure 2.1) I observed that terrestrial carcasses of birds (naturally occurring carcasses and not those used in the experiment) were scavenged by land crabs. These naturally occurring cadavers were quickly skeletonised by large numbers of crabs "picking" off the flesh (Figure 2.3).

Molluscs.

Gastropods (crown conch, *Melongena corona*) were observed to rapidly strip carcasses of birds of soft tissues (Chapter 2). Carnivorous/scavenging gastropods are not uncommon. Taylor (1981) stated that there are many modern marine species of flesh eating gastropods and that they can be traced through geological time to their origin during the late Cretaceous. Thus

cadavers in the marine environment, where these types of gastropod occur, will be skeletonised rapidly and subsequent rates of disarticulation and transport will be quicker.

Other researchers have noticed that scavengers quickly remove bird carcasses from terrestial environments. Rosene and Lay (1963) reported that of sixty Bobwhite Quail (*Colinus virginianus*) carcasses that they placed in agricultural fields in Alabama and Texas, 25-50% disappeared completely within four days due to the activities of scavengers. Some individuals disappeared completely within 24 hours, and after 30 days there were virtually no traces of any of the 60 quail. Balcomb (1986) placed carcasses of 78 songbirds (mainly passerines) in corn fields a few days after planting. After five days, 72 carcasses had been removed by scavengers, and from this and other data Balcomb (1986) concluded that the average time a carcass survived was about 1.2 days. The rate of carcass disappearance was greatest during the first 24 hours, and over half the carcasses were totally removed without a trace (i.e. not even a feather remained). Tobin and Dolbeer (1990) found that bird carcasses disappeared from cherry and apple orchards within 8-10.5 days, on average, due to scavenging activity. Ground cover did not affect the duration of carcass survival.

4c2. Temperature

Where the temperature is higher the rate of decay is quicker. The difference between the sub-tropical environment of southern Florida where the average air temperature was 31°C and the cool temperate environment of England, where the average air temperature was about 18°C were chosen to perform a simple 'experiment'. This 'experiment' involved placing a bird in each locality (one was the mangrove forests of Florida and the other was in a deciduous woodland in Warwickshire) which was protected from large scavengers (by using the cages described in Chapter 2), as these will quickly mask any effects of temperature, and then observing how long it took for the soft tissues to decay to liquid. The observation of two cadavers in these environments showed that in Florida the soft tissue of a bird decayed away after only two days whereas in England the same size of bird took at least five days to reach the same state of decay.

Temperature affects the rate of decay of soft tissues because the more rapidly the optimum temperature for the growth of decay bacteria and the action of autolytic enzymes is reached, the quicker the tissues will decay.

The impact of temperature and scavenging on the fossil record of birds has been described in Chapter 2.

4d. The Disarticulation of Birds

The disarticulation of bird carcasses was monitored at Blithfield Reservoir, near Rugeley, Staffordshire (Figure 4.4). The reservoir was visited every spring (May) for three years. This policy was adopted because any winter mortalities would still be found on the shoreline, and because the water level had started to drop from its winter maximum so creating a strandline of debris in which the carcass were found. The shoreline was intensively searched for dead birds/skeletons/disarticulated bones. Birds were observed in a variety of states of disarticulation. The results from this study can be seen in Table 4.2.

These results can be placed in the morphological decay stages defined in Chapter 2. Figure 4.5 shows the carcass of a magpie (*Pica pica*) found on the shoreline of the reservoir. By searching the area around the carcass other remains of the magpie were discovered (Figure 4.6). The magpie has disarticulated to morphological decay stage 4 (Chapter 2), i.e. the skeleton has disarticulated fully and bones are being transported away from the site of disarticulation (as a result of wind-induced waves which wash against the shoreline). The shoreline also yielded three complete and articulated black headed gull (*Larus ridibundus*) wings (humerus, radius, ulna, metacarpals, phanages). This supports the observation that these bones are the last to disarticulate (morphological decay stage 3g, Chapter 2).

It is possible to infer biostratinomic data from the numbers and types of isolated bones that were found around the shoreline. In total ten isolated bones were found (this represented a complete day of searching the strandline): two skulls, two humeri, one radius, four sterna, and one synsacrum (pelvis). From the Voorhies grouping of avian skeletal dispersal groups derived from the study by Napawongse (1981) (Table 1.4) it is evident that seven out of these ten bones are Group III (lag deposits), and the other three are Group II (removed gradually, by traction). Transport on the shoreline of the reservoir was gentle (low velocities) as it is the result of wind-induced waves only. This is consistent with the placing of the above skeletal elements in Groups II and III (Chapter 1).

The isolated bones also show signs of predation/scavenging and abrasion. The humerus of a black headed gull (*Larus ridibundus*), for example, was fractured in the middle of the shaft by the biting action of a predator/scavenger (possibly a red fox) (Figure 4.7). This was deduced from the fracture morphology which showed a spiral fracture (*sensu* Marshall, 1989), a XCH fracture according to the classification system of Davis (1985) (X = mixed fracture orientation; C = medial fracture surface location; and H =

curved fracture shape) which is indicative of scavenging activity upon "fresh" bones.

The bed and shoreline of the reservoir is comprised mainly of sand and gravel, so any bone transported by traction or saltation is severely abraded. Figure 4.8 shows sternum fragments of three black headed gulls that were collected from the shoreline of the reservoir. They show extensive effects of abrasion; the bones fall into Voorhies' (1969) Group III indicating that transport was by saltation/traction (Table 1.4). The costal margins of the sternum have been fragmented/destroyed, the carinal apex has been damaged and the thin bone of the sternal plate has been perforated. As these bones fall within Voorhies Group III (lag deposits), they would be infrequently transported; thus the damage to them must have resulted from only a short period of transport. This corresponds with Napawongse's (1981) results, and explains why these skeletal elements are scarce in geological deposits where high energy transport has occurred, e.g. the La Meseta Formation (Chapter 6).

4e. The Decay of Feathers

The preservation of feathers is dealt with in Chapter 5. This section deals with observations of the decay of feathers in the natural environment.

Data on feathers were collected at Blithfield Reservoir (Figure 4.4). Due to a fall of one metre in the water level during the spring/summer months a strandline was created, hence the reason for conducting the collection during May 1992. This strandline was approximately two metres wide and stretched along the whole shoreline. The strandline yielded large numbers of isolated feathers. Six sites along this strandline were chosen for the sampling of feathers. The selection of sites was determined by their accessibility. These six sites consisted of a one metre square area within the boundaries of the strandline. From the one metre square all the feather material that was present was collected. The six sites (i.e. $6m^2$) yielded 239 feathers (see Table 4.3).

By calculating the area of the strandline (length of strandline multiplied by width of the strandline) and then by multiplying by the average number of feathers per $metre^2$ it is estimated that over 414,000 feathers were present along the length of the strandline. This implies that feathers are exceptionally abundant in the natural environment, but in fact this assumption would be erroneous as it is more likely that this large number of feathers represents an accumulation of feathers over time as a result of their very slow degradation. This is supported by the fact that only 0.8% (n=239) of the feathers were pristine i.e undecayed, suggesting that the feathers had been decaying on the

strandline at least since the the birds last moulting period some 7 to 8 months previously.

All the feathers collected were contour feathers; 89% (n=239) were primary and secondary flight contour feathers (see Chapter 5, for the morphology of feathers). This indicates a large bias towards flight contour feathers, as this group represents only approximately 0.7% of the total number of feathers on an individual bird (Brown *et al.*, 1987). Therefore it appears that primary and secondary flight contour feathers have been concentrated on the strandline. To examine this result a simple experiment was undertaken. Ten flight contour and ten semiplume feathers, freshly plucked from a black headed gull (*Larus ridibundus*), were placed in a circular flume tank. The water velocity was 0.4 m/s. The semiplume feathers sank rapidly (all had sunk to the bottom of the tank after 30 seconds), but the flight contour feathers were observed to float until the experimental run ended (3 hours). This can be explained by the fact that these feathers have a large rachis (Figure 5.1) which contains a lattice work of air pockets. These air pockets render the feather very light, which in turn enables it to float. The wind induced surface currents of the reservoir then could have driven these feathers to the shore where they are deposited on the strandline. The other types of feather do not have a large air-filled rachis and only float whilst the vane portion of the feather creates a large surface area to distribute the weight of the feather. Therefore when this vane portion becomes matted together from the action of the water, the large surface area of the feather (relative to the weight) is lost and the feather sinks. Such feathers are therefore rarely transported to the strandline unless they are shed very close to the shoreline.

For a feather to be fossilised it needs to reach the lake bed (Chapter 5); therefore the fossil record of feathers should be depauperate in primary and secondary flight contour feathers. A survey of fossil feather collections in museums (which took the form of photographing, documenting and classifying in morphological types all the fossil feathers in the collections of the Smithsonian Institution, Natural History Museum, and the Landesmuseum (Darmstädt), i.e the three largest repositories of fossil feathers) confirms this prediction; they form only 12% (n=83) of all isolated feathers surveyed (see Table 4.4).

Observations on the abundant primary and secondary flight contour feathers collected from Blithfield reservoir allowed six decay categories to be identified (Figures 4.9 and 4.10).

1. The feather is pristine and shows only slight matting of barbs caused by transport (Figure 4.9).

2. The feather barbs have become more matted and show abrasion at their tips. Some have been removed from the rachis. The rachis shows signs of cracking along its axis (Figure 4.9).

3. The barbs of the feather are very damaged. The distal rachis becomes bent and very brittle. The proximal rachis shows large splits along its axis (Figure 4.9).

4. The barbs of the feather have been removed almost completely; only short portions remain. Large scale cracking of the rachis occurs (Figure 4.10).

5. No barbs remain on the rachis. The distal rachis has split and only fragments remain. The rachis is extremely brittle (Figure 4.10).

6. Only the most proximal portion of the rachis remains. This shows extensive splits and is "paper" thin and extremely brittle (Figure 4.10).

Only one fossil feather shows any signs of the above decay categories (Figure 4.11) implying that fossilisation takes place rapidly (Chapter 5) or that decay takes place very rapidly. The fossilisation of feathers requires bacteria (Chapter 5) but S.E.M. analysis of the above decaying feathers shows little bacterial action. It is therefore assumed that the terrestrial degradation of feathers is caused mainly by sunlight. To test this assumption a freshly plucked flight contour feather (from a pigeon *Columba palumbus*) was placed in a window for 14 months. After this period of time the feather had become exceptionally brittle, exactly like those in decay categories 5 and 6. It must be pointed out that glass filters sunlight (decreases levels of UVa and UVb) and that the time taken to degrade the feather through glass is probably less than that in natural situations.

SPECIES	MEAN ANNUAL ADULT MORTALITY (%)	MEAN FURTHER LIFE (YEARS)	U.K. POPULATION	YEARLY MORTALITIES IN U.K.
Fulmar *Fulmarus glacialis*	6	16.2	60,000	36,000
Canada Goose *Branta canadensis*	16	5.6	10,000	1,600
Swift *Apus apus*	18	5.6	200,000	36,000
Rook *Corvus frugilegus*	25	3.5	3,000,000	750,000
Herring gull *Larus argentatus*	30	2.8	600,000	180,000
Wryneck *Jynx torquilla*	33	2.5	20	7
Skylark *Alauda arvensis*	33	2.5	6,000,000	1,980,000
Turtle Dove *Streptopelia turtur*	50	1.5	250,000	125,000
Starling *Sturnus vulgaris*	53	1.4	14,000,000	7,420,000
Robin *Erithacus rubecula*	62	1.1	10,000,000	6,200,000

TABLE 4.1 **Bird Mortalities of British Bird Species (adapted from Welty and Baptista, 1988; Gooders, 1987).**

Common Name	Latin Name	Skeletal elements recovered	Morphological decay stage	Damage to bones
Black Headed Gull	*Larus ridibundus*	Complete, articulated skeleton with soft tissues and feathers	1	None
Black Headed Gull	*Larus ridibundus*	Complete, articulated skeleton with soft tissues and feathers	1	None
Black Headed Gull	*Larus ridibundus*	Complete, articulated skeleton with feathers	1	None
Black Headed Gull	*Larus ridibundus*	Complete, articulated skeleton with feathers	1	None
Black Headed Gull	*Larus ridibundus*	Complete, articulated skeleton with feathers	1	None
Black Headed Gull	*Larus ridibundus*	Articulated wing: humerus to phalanges	3g	None
Black Headed Gull	*Larus ridibundus*	Articulated wing: humerus to phalanges	3g	None
Black Headed Gull	*Larus ridibundus*	Articulated wing: humerus to phalanges	3g	None
Magpie	*Pica pica*	2 humeri, 2 ulnae, 2 scapulae, 2 coracoids, sternum, 5 thoracic vertebrae, 8 ribs, synsacrum, femur, tibiotarsus	4	None
?	?	Partial skull	5	Abraded and broken
?	?	Partial skull	5	Abraded and broken
Black Headed Gull	*Larus ridibundus*	Humerus	5	Broken, see Figure 4.7
?	?	Humerus	5	None
?	?	Radius	5	None
?	?	Synsacrum	5	Abraded
?	?	Sternum	5	Abraded
Black Headed Gull	*Larus ridibundus*	Sternum	5	Abraded, see Figure 4.8
Black Headed Gull	*Larus ridibundus*	Sternum	5	Abraded, see Figure 4.8
Black Headed Gull	*Larus ridibundus*	Sternum	5	Abraded, see Figure 4.8

Table 4.2 **Skeletal specimens recovered from the strandline of Blithfield Reservoir, Staffordshire.**

Site	Wing Contour Feathers	Body Contour Feathers	Other Feathers
BFCS 1	29	5	0
BFCS 2	13	1	0
BFCS 3	30	3	0
BFCS 4	24	5	0
BFCS 5	32	6	0
BFCS 6	85	6	0
Total number of feathers	213	26	0
Percentage of sample (n = 239)	89	11	0

Table 4.3 **Numbers of feathers recovered from the six 1m² sample sites at Blithfield Reservoir, Staffordshire.**

Locality	Number of Wing Contour Feathers	Number of Body Contour Feathers	Number of Semiplume Feathers	Number of Down Feathers	Number of Other Feathers
Green River Fm., Eocene, Wyoming, USA.	2	18	14	1	0
Florissant Fm., Oligocene, Colorado, USA.	6	1	4	0	0
Calvert Fm., Miocene, Maryland, USA.	0	5	0	0	0
Salt Lake Group, Pliocene, Utah, USA	1	4	0	0	0
Fort Union Fm., Paleocene, Montana, USA	1	0	0	0	0
Messel, Eocene, Germany	0	23	2	0	0
Total Number	10	52	20	1	0
%'age of Total (n = 83)	12%	63%	24%	1%	0%

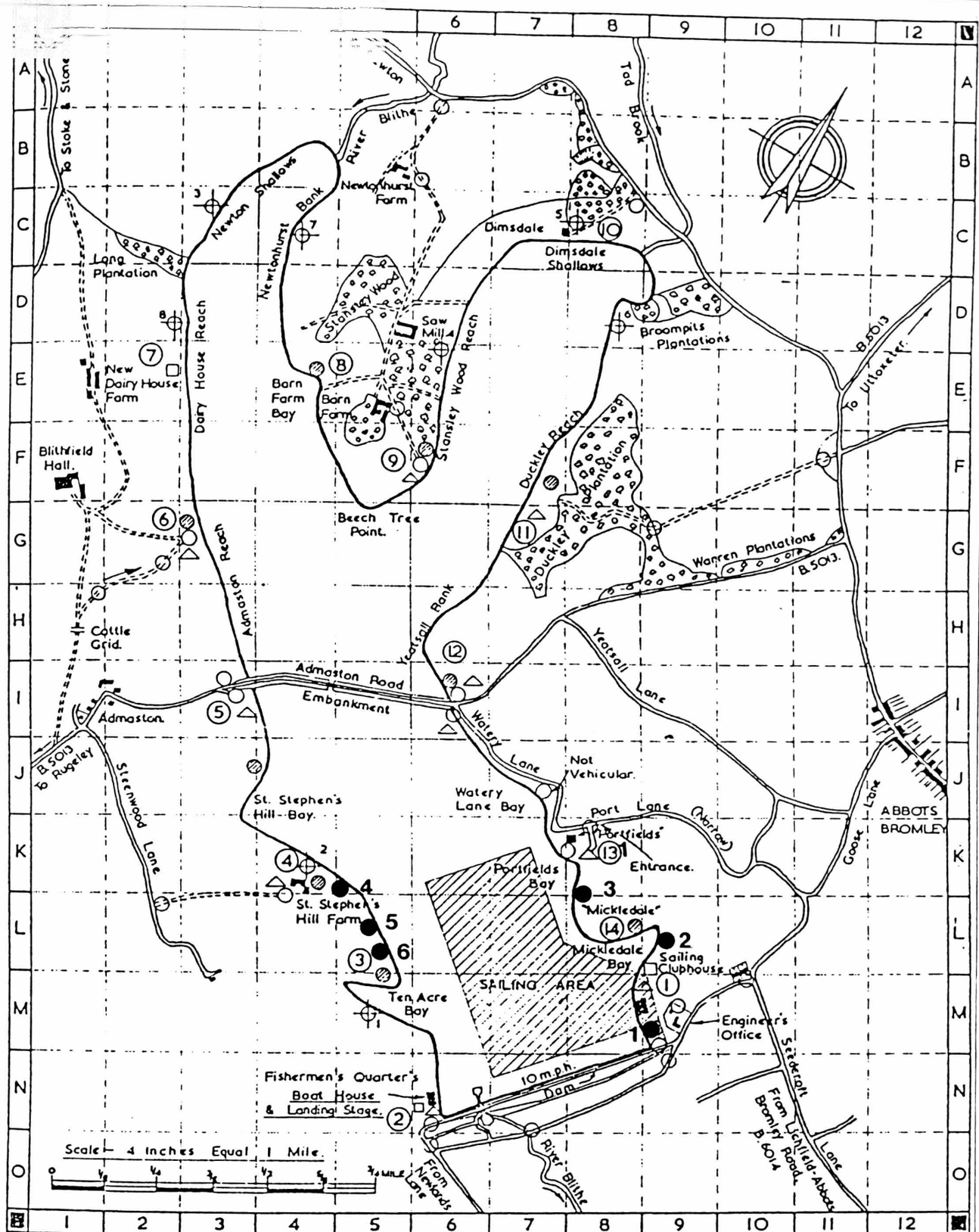
Table 4.4 **Numbers of isolated fossil feathers placed into different morphological categories.**

FIGURE 4.1 A giant petrel (*Macronectes giganteus*) killing a young Adélie penguin chick (*Pygoscelis adeliae*). The petrel has chosen a smaller, weaker bird that has still to moult its down feathers. Photograph by Ben Osborne and courtesy of the B.B.C. Natural History Unit.

FIGURE 4.2 A carcass of a woodpigeon (*Columba palumbus*) that has been killed by a domestic cat (*Felis domesticus*). The carcass was very fresh and blow flies (Family: *Calliphoridae*) and wasps (*Vespula* sp.) were feeding on the exposed flesh. The blow flies had also laid eggs on the carcass. The carcass also shows the disarticulation caused by predation. The head has been removed and the pectoral girdle has been disarticulated (the broken shaft of the humerus can be observed). This pattern is caused by the cat killing the pigeon by biting the head off and then eating the thoracic region.

FIGURE 4.3 The remains of a brown pelican (*Pelcanus occidentalis*) that has been scavenged by land crabs. Note that the skeleton has been totally stripped of any soft tissue yet the skin (with feathers still attached) has not decayed or been eaten.

FIGURE 4.4 Blithfield Reservoir, near Rugeley, Staffordshire. The black circles show the six feathers sites. The area surveyed was the reservoir shoreline south of Admaston Road embankment. Map courtesy of Severn Trent Water Authority (drawing number BR 2990/6).



DISTANCES FROM BLITHFIELD RESERVOIR.

BIRMINGHAM	26 MILES.
BURTON-UPON-TRENT	12 "
DERBY	22 "
STAFFORD	14 "
WOLVERHAMPTON	21 "

REFERENCE.

ENTRANCE GATE	○
HARD STANDING FOR CARS	△
LAVATORY / SHELTER	⊘
LAVATORY	□
BIRD WATCHING HIDES	⊕

FIGURE 4.5 (top)

The bones of a magpie (*Pica pica*) as discovered on the shoreline of Blithfield reservoir (at St. Stephen's Hill Bay). The photograph shows the sternum and other elements of the pectoral girdle.

FIGURE 4.6 (bottom)

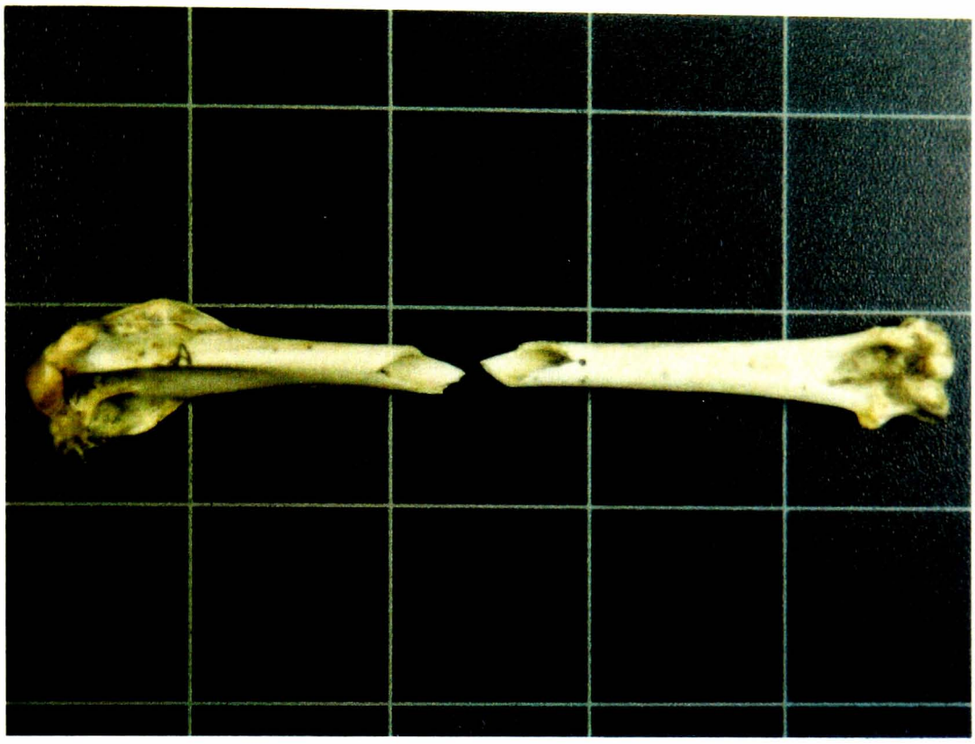
After searching the immediate vicinity of the initial find of the magpie skeleton (Figure 4.5) other bones were discovered. The photograph shows all the bones recovered placed into correct anatomical position. The disarticulation of the skeleton was gradual and wave transport was dispersing the skeletal elements along the shoreline.

FIGURE 4.7 (top)

The humerus of a black headed gull (*Larus ridibundus*) fractured in the centre of the shaft. The fracture was probably caused by the predation/scavenging action of a red fox (*Vulpes vulpes*). The fracture is classified as a spiral fracture (*sensu* Marshall, 1989) and as a XCH fracture (*sensu* Davis 1985). This indicates scavenging activity upon "fresh" bones.

FIGURE 4.8 (bottom)

Three sterna showing increasing abrasion. Sternum a shows damage to the costal margins and perforation of the sternal plate. Sternum b shows further damage to the costal margins and the distal and proximal portions of the sternal plate have been destroyed. The carinal apex shows signs of damage. Sternum c shows that a costal margin has been removed from the sternum by abrasion.



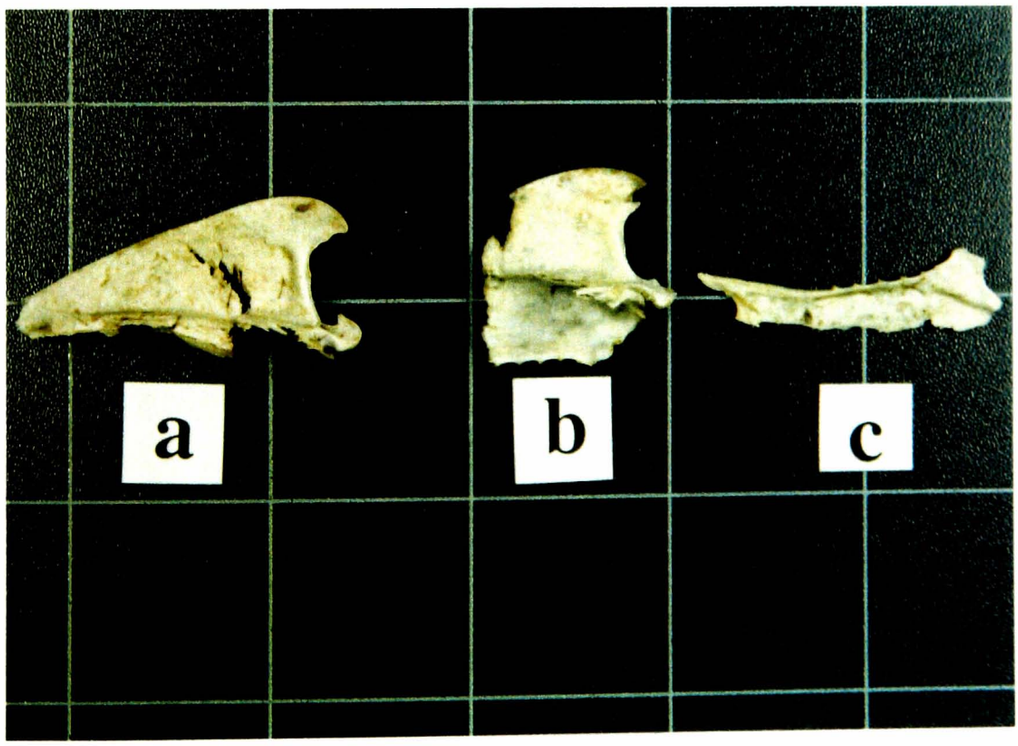

a
b
c

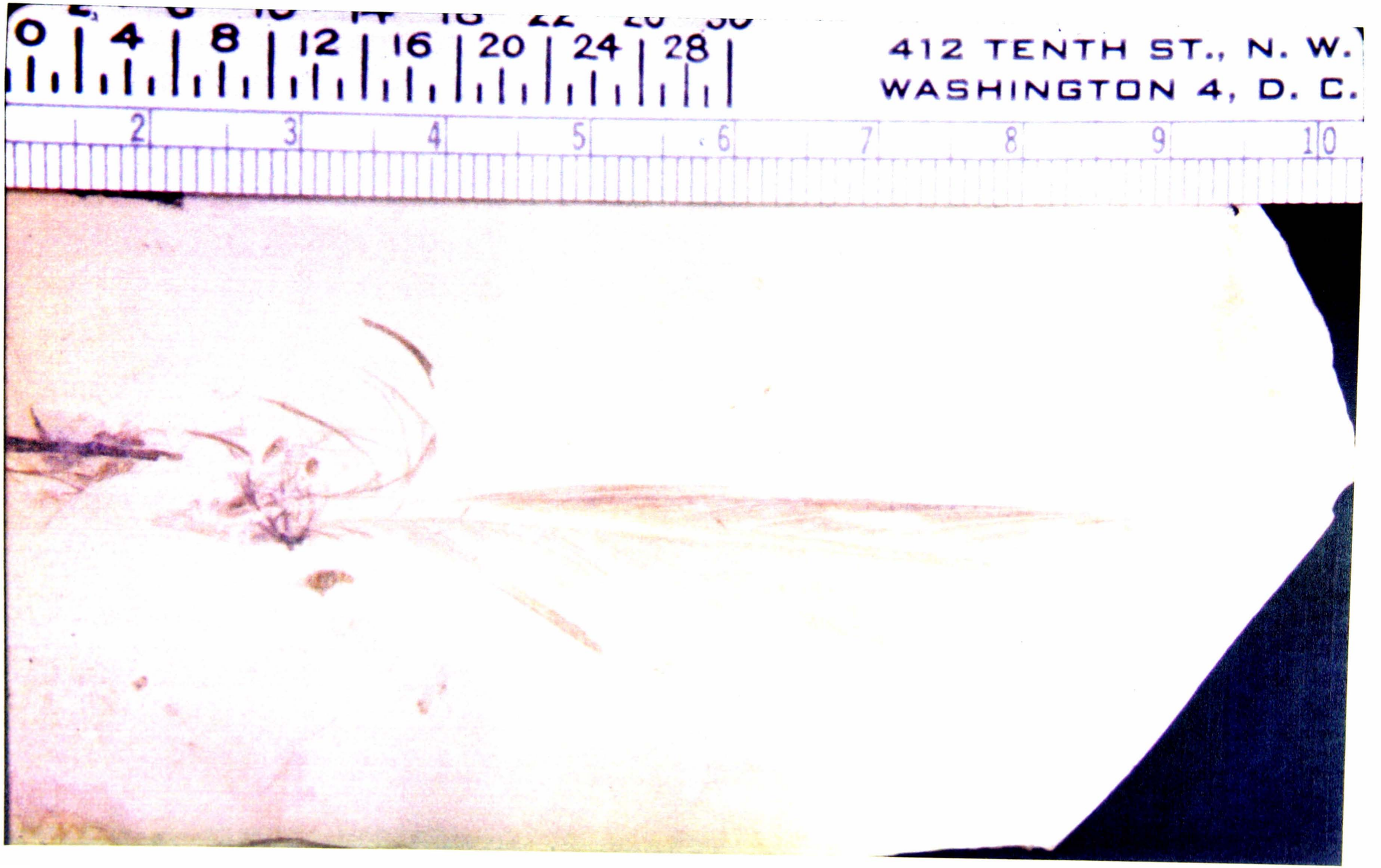
FIGURE 4.9 (top) Feathers collected from Blithfield reservoir. The numbers refer to the feather decay categories 1, 2, and 3 described in the text.

FIGURE 4.10 (bottom) Feathers collected from Blithfield reservoir. The numbers refer to the feather decay categories 4, 5, and 6 described in the text.

1
2
3

4
5
6

FIGURE 4.11 An isolated flight contour feather (USNM 276757) from the Eocene, Green River Formation of Wyoming. The feather can be assigned to decay stage 2. It shows damage to the vanes along the trailing edge. This can be compared to Figure 4.9 (feather 2).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Chapter Five
The Taphonomy of Feathers

5a. Introduction

Feathers are diagnostic of the Class Aves. There is no extant species of bird that does not have feathers and this is also assumed to have been true of extinct species. It has also been speculated that feathers may have been present in some dinosaurian genera (Bakker, 1986; Paul, 1988).

Fossil feathers are not uncommon. They first appear in the fossil record in the Tithonian (Late Jurassic) and belong to the first recognised bird, *Archaeopteryx lithographica* (Meyer, 1860). Isolated feather finds have been reported from the Cretaceous (eg. Talent *et al.*, 1966; Martill and Filgueira, 1994; Kellner *et al.*, 1994), and they become more abundant in the Caenozoic especially in freshwater bodies, where they commonly occur in association with fossil insects and fish.

Bird carcasses can disarticulate quickly; they can be reduced to ten percent of their original body mass, for example, within thirty days (Chapter 2b6). Schäfer (1972) noted that the sub-aqueous portion of herring gull carcasses floating in the sea had lost all feathers, including the primary and secondary contour feathers of the wing, after thirteen days. However Chapter 2 showed that the ligaments, which hold the primary and secondary contour feathers to the ulna, are recalcitrant and may still attach these feathers after 56 days of decay, sometimes long after skeletal disarticulation has occurred. Most occurrences of feathers in the fossil record are, however, single isolated specimens and probably represent feathers lost during the bird's lifetime by preening or moulting, for example.

5b. The Morphology of Feathers

The number of feathers on a bird depends mostly on its size. For example, there are approximately 1,500 feathers on a swallow *(Hirundo rustica*) and about 25,000 on a Bewick swan *(Cygnus columbianus)* (Brown *et al.* 1987). However numerous, all feathers fall within five well-defined categories (Figure 5.1).

1. Down feathers have a small calamus and a weak or absent rachis. The barbs remain separate, with filamentous side branches. The whole feather is very light and fluffy and acts as an insulator against heat loss.
2. Filoplumes are like fine hairs, consisting of a calamus and a rachis which are sometimes tipped with a tuft of barbs. They grow among the other feathers of the plumage. One possible explanation of their

function is to aid the bird in positioning the outer feathers during preening.

3. Bristles occur on the head and neck, particularly around the eyes and the corners of the mouth. They consist of a stiff rachis which is usually naked or with only a few barbs near the tip.
4. Semiplumes have a well developed rachis, but no stiff vane; they are entirely downy. Semiplumes may have a small afterfeather which is attached at the superior umbilicus.
5. Contour feathers comprise all of the visible plumage of an adult bird and also give the body its form. They grow in distinct rows or tracts known as pterylae. They are separated by spaces known as apteria within which usually grow semiplume and down feathers. These feathers have a well developed rachis, with barbs linked together (by a series of barbules and hamuli) to form a flat surface called the vane. At the base the barbs are usually separate and downy. Contour feathers can also have an afterfeather which is attached at the superior umbilicus. The flight feathers of the wing and the large feathers of the tail are contour feathers.

5b1. The Taxonomic Assignment of Feathers

Isolated feathers may be identified to taxon using the colouration and morphology in combination, but it is impossible to identify fossil feathers as the colouration does not preserve. The two exceptions (from the Cretaceous Crato Formation of Brasil (Martill and Frey, 1995) and from the Eocene Grube Messel deposits) preserve apparent evidence of differences in pigmentation along a feather, although the colour has long since gone (Figure 5.2). It is suggested here that feathers should not be assigned to specific taxa (i.e. given binomial Latin names) as this does nothing to aid avian taxonomy. Feathers should be categorised based on morphology only, i.e. assigned to the five categories above. *Archaeopteryx lithographica* was originally described on the basis of a single flight contour feather (Meyer, 1860). The association of a binomial latin name with this feather creates taxonomic problems because (for the reasons mentioned above) it can never be related to the skeletal remains of *Archaeopteryx*. Hence, while the name needs to be retained for the skeletal specimens, the isolated feather should be reclassified as Fossil Feather: Contour (Flight).

5c. The Structure and Bacterial Degradation of Feathers

Feathers are made from keratin, a protein with a rigid structure. The fibrous component of the keratin is a complex helical structure derived from ß-

pleated sheet proteins (Wainwright *et al.* 1982). This structure is due to a crystalline polymeric fibre which is embedded in a highly cross-linked amorphous polymer matrix. Although keratin is resistant to decay, it does not normally accumulate in nature. It is not degraded by common bacterial proteolytic enzymes such as trypsin, pepsin, and papain, but keratinolytic activity has been reported in species of *Aspergillus* (Koh *et al.* 1958), *Ctenomyces* (Sen Gupta *et al.* 1950), *Streptomyces* (Noval and Nickerson 1959) and *Bacillus* (Molyneaux 1959). These species of bacteria all degrade wool keratin which is slightly different from feather keratin. Only recently has a bacterium (*Bacillus licheniformis* PWD-1) been isolated that degrades feathers (Williams *et al.* 1990), but it only degrades feathers that have been steam treated or autoclaved making the keratin available for hydrolysis by the bacterium. Thus there must be other as yet unidentified bacteria active in sedimentary environments which can decay this group of proteins naturally. *Bacillus licheniformis* PWD-1 functions in both aerobic and anaerobic conditions to a similar degree although it occurs naturally in the anaerobic conditions of poultry waste (Williams *et al.* 1990).

A very important factor in the bacterial degradation of feathers is the formation of bacterial glycocalyx. The majority of bacteria (both gram positive and gram negative) in the natural environment grow in glycocalyx enclosed microcolonies attached to inert surfaces. This mode of growth enables the bacteria to occupy and persist in a suitable ecological niche, and their fibrous anionic glycocalyx serves both to trap nutrients and cations (Figure 5.3), by acting as an ion exchange resin, and to protect them from attack by bacteriophage and phagocytic cells (Cheng *et al.* 1981). Glycocalyx is predominantly made of exopolysaccharides which bind to the outer cell wall surface of the bacteria (Costerton *et al.* 1981). The glycocalyx is often comprised of a fibrous matrix 0.5-1.0 μm in width (Bayer and Thurrow 1977, Mackie *et al.*, 1979) and in specialised cases, bacteria that digest insoluble nutrient substrates such as cellulose (and possible feather keratin) are able to attach specifically to their nutritive substrate (Patterson *et al.*, 1975, Minato and Suto 1976). These types of bacteria use their enveloping glycocalyx matrix so that surface-bound enzymes can digest the substrate (Cheng *et al.*, 1977), and to bind and channel the resultant soluble nutrients back to the bacterial surface (Costerton *et al.*, 1978). These chemical transfer effects may be important in the lithification of bacteria and also the preservation of the glycocalyx within the fossil record.

5d. The Morphological Types of Preservation

5d1. Type A: Bacterial Autolithification

In this type of preservation the outline of feathers is represented by bacteria and their glycocalyx.

Bacterial autolithification is the characteristic mode of preservation of soft tissues at Grube Messel (Wuttke, 1983, 1988; Franzen, 1990). Individual organs are not preserved, but the outline of the soft tissue is apparent as a "shadow" around the specimen in siderite (Wuttke, 1983). The preservation of soft tissues in this way at Messel is restricted to a light brown to brown, dense, clearly laminated freshwater pelite (facies three of Franzen *et al.*, 1982).

The bacteria which colonised the feathers in Lake Messel may have been either aerobes or anaerobes. The preservation of the bacteria and their glycocalyx, however, indicates that autolithification occurred within the methanogenic zone of the sediment (based on Wuttke's (1983) model for siderite lithification, Figure 5.4). The water of Lake Messel was obviously oxygenated, based on the diversity of aquatic life that it supported (Schaal and Ziegler, 1992). The oxic/anoxic interface lay at the sediment/water interface or just above it. As siderite precipitation requires a reducing Eh it must have formed within the anoxic sediment. Bacterial autolithification may have occurred as sediments enclosed the feather and conditions became anoxic, the change in conditions promoting siderite precipitation (Wuttke, 1983).

The bacteria are simple rod-shaped structures corresponding to Wuttke's (1983) Type 1. They are aligned parallel and end-to-end giving the appearance of a "flowing mat" (Figure 5.5). This pattern does not reflect the structure of the feather and may simply be the arrangement which ensured maximum bacterial contact with the nutritional substrate (Wuttke, 1983). It suggests that the bacteria were lithified in life position. This should be expected if they were killed by the autolithification process which occurs almost instantly (but the bacteria that become autolithified might not be first generation bacteria because, although the autolithification is instantaneous, it may be some time before conditions are correct for this process to occur).

5d2. Type B: Carbonised Trace

This style of preservation is characterised by carbonised traces in fine grained mudrocks.

A flattened "honeycomb" texture similar to that described for type-A preservation is evident under the SEM (Figure 5.6). It may represent the glycocalyx left behind by bacteria that degrade feathers. Possible traces of

autolithified bacteria are evident (Figure 5.6). The bacteria that metabolise the feather produce a glycocalyx which is then flattened and carbonised with diagenesis. It is possible that the feather undergoes kerogenisation (thermal degradation of the keratin) in some instances, although in the specimens examined the texture found was that of a flattened bacterial glycocalyx.

The glycocalyx occurs in two forms. The first form is found growing completely over the feather and surrounding sediment (Form I). It is not possible to delineate where the original edge of the feather began. The second form occurs only on the feather itself and hence it is possible to see the outline of the feather, even the individual barbs (Form II). The two types of fossil glycocalyx indicate that conditions for bacterial growth differ (even within the same specimen). Form I indicates optimum bacterial growth, where the bacteria not only colonise the feather but also the surrounding substrate, which may indicate that the bacterial species are also able to utilise other tissue proteins. Form II glycocalyx indicates that the bacteria had only colonised the feather when bacterial growth was arrested, or that the bacterial type was totally specialised to feather proteins, or that there was nothing beyond the feather for the bacteria to colonise.

It can be assumed that, in this most common type of feather preservation, the bacteria themselves were destroyed at or before the lithification process, whereas the glycocalyx (a recalcitrant bacterially-produced substance) remains. The diagenesis of this organic compound (in modern glycocalyx it is predominantly exopolysaccharides) results in the preservation of a trace of the feather impressions.

5d3. Type C: Imprintation

The Solnhofen Limestone deposits of Bavaria contain the most famous of all fossil feathers, those of *Archaeopteryx lithographica*. The preservation of these feathers was traditionally considered to reflect "impressions" of the feathers on the soft sediment surface (eg. de Beer 1954). Rietschel (1985) noted that this was not compatible with recent understanding of the deposition of the Solnhofen Limestone and argued that preservation could only have occurred in one of two ways, the plumage by being covered with very fine grained sediment or with an overgrowth of bacteria and algae. Rietschel (1985) termed these mechanisms "precipitation", as distinct from impression as the end result is an external mould on both the slab and counter slab.

The preservation of the feathers of *Archaeopteryx* is unusual. The first feather to be described (Meyer 1860), on which the species and genus were based, is taphonomically unusual. It appears to be characteristic type-B preservation (from observation of photographs) whereas in all the skeletal

specimens with feather "impressions" are type-C preservation. Type C preservation also depends upon bacterial action. S.E.M. investigations (two samples from the London specimen, BMNH 37001 were examined, the original location of the samples can be seen in Figure 5.7) of the feather material of the London *Archaeopteryx* (Figures 5.8 and 5.9) show lithified bacteria and glycocalyx textures similar to those found in type B preservation. However the actual mechanisms of fossilisation by these types of bacteria are completely different.

Type C preservation involved a specific sequence of processes. The ventral side of the *Archaeopteryx* feathers were in contact with the substrate. In this environment feather-degrading bacteria proliferated and colonised the substrate and the ventral side of the feathers. The feathers were then covered with further sediment. The action of the bacteria and the glycocalyx within the sediment created conditions which allowed early diagenetic minerals to be formed. Before the sediment in contact with the ventral side of the feathers was fully hardened the weight of the overlying sediment had impressed the feathers into this substrate. Then, when the early diagenesis of the substrate occurred, it retained the impression of the ventral surface of the feathers. When the feather finally decayed away, the soft sediment above (unaffected by the early diagenesis, as not in contact with the bacteria) was pressed into the mould, created by the ventral side of the feathers, by the weight of the overlying sediment.

This model explains why in all the *Archaeopteryx* specimens the slab contains a mould of the ventral surface of the feathers and the counter-slab contains a cast of the same ventral side of the feathers (this effect was noted by Rietschel (1985) and termed the double strike effect). Further evidence for this model is derived from the examination of other Solnhofen fossils which reveal, in a large number of specimens, a smooth layer around the fossil (on the surface upon which the organism came to rest) which indicates microbial activity (Seilacher *et al.*, 1985). A very fine layer of sediment can be seen adhering to parts of all the *Archaeopteryx* feather impressions. This layer contains much more detailed impressions of the feather structure and it is postulated here that it represents remnants of the original early diagenetic layer of lithified bacteria and glycocalyx.

5d4. Type D: Enclosed in Amber

The most perfectly preserved fossil feathers are those enclosed in amber. It is probable that the feather is unaltered from its original state apart from some dehydration of the keratin polymer, as occurs in amber-preserved insects (Henwood 1992). All feathers that have been found in amber so far,

are down and contour feathers (Figure 5.10). This suggests two possible mechanisms for their entrapment: either the bird brushes past the resin and some feathers are detached, or preening activities of the birds produce loose feathers which stick to the resin.

Feathers in amber are not uncommon (approximately 0.01 specimens per kilogram of amber, locality 9, Figure 5.11 (Pike, 1992)). Three localities are known at present (Figure 5.11) that produce feathers; they are associated with diverse insect assemblages.

5d5. Type E: In Coprolites

This preservational style is characterised by three-dimensional "feather voids" within phosphatic coprolites.

This preservational style has been reported so far only in the marine Miocene Chesapeake Group of Maryland in the USA (Wetmore 1943). It is also noteworthy that this locality is only one of two known fossil feathers sites from a marine environment and is the only one which is well documented and available for study. The other being Williston (1896) who described feather material from the Kansas Chalk (now the Niobrara Formation; Bennett, 1990) but the location and validity of this report is unknown.

The feathers are found within coprolites, probably those of a large carnivore such as a fish, whale or crocodile. It is likely that the bird was eaten whole and the undigested feathers were excreted by the animal.

The feathers appear as external moulds (Figures 5.12 and 5.13) within the phosphatic coprolites. There are no bones or other material within the coprolite (S.J. Olson, pers. comm., 1992, stated that the coprolite had been dissected and X-rayed and nothing but feather material had been found within). The faecal mass would have started to undergo diagenesis once it was on the sea floor. The feather would have remained inside the coprolite whilst digestion and excretion were taking place. Once the coprolite reached the sea bed the enzymes and the bacteria of the intestines would still be active and would metabolise the feather, leaving a three-dimensional void within the faecal mass. Early diagenesis of the coprolite had occurred before compaction so the three-dimensional shape was retained. Prévôt and Lucas (1991) described the diagenesis of phosphatic fossils and showed that bacteria promoting decay (in this case the decay of the coprolite) would release PO_4^{3-} creating locally acidic conditions. These acidic conditions would liberate Ca^{2+} present in any local calcium carbonate (e.g. shell debris, microfossil tests etc.). The newly liberated Ca^{2+} and PO_4^{3-} would combine to form calcium phosphate (apatite). This phosphatising mechanism must have

occurred rapidly because the form and structure of the coprolite was maintained as soon as the material was defacated.

5e. Distribution of Fossil Feathers

Inhibition of decay is the most important factor in the preservation of soft tissues. Such conditions occur in some Konservat Lagerstätten deposits. There are a number of factors which favour feather preservation. The most important of these is to allow feather-degrading bacteria to grow. This statement may seem incompatable in light of the first two statements but it emphasizes that some decay is necessary to promote mineralisation (Briggs and Kear, 1993). Therefore it is pssible to identify environments in which feather preservation can take place.

Figure 5.11 and Table 5.1 show all the known fossil feather localities. Figure 5.14 show these localities grouped into six sedimentary environments:

1. Amber (Terrestrial)
2. Lacustrine
3. Swamp
4. Coastal Lagoon/ Estuarine Flats
5. Restricted Marine
6. Marine

This diagram can be compared with Figure 5.14 which shows the same data except that the localities are grouped by preservational styles instead of sedimentary environment. From the comparison of these two diagrams it is evident that preservational styles are linked directly to sedimentary environments. There are two examples, however, which depart from this relationship: Messel and Solnhofen. The preservational styles bacterial autolithification (Type A) and imprintation (Type C) are found only at Messel and Solnhofen respectively. It is evident that bacterial autolithification and imprintation are closely linked to the carbonised trace style (Type B) because all three require the formation of bacterial glycocalyx. It therefore can be inferred that bacterial autolithification and imprintation are exceptionally preserved forms of carbonised trace preservation i.e. where decay has been inhibited earlier than usual by mineralisation. Within Grube Messel and Solnhofen (where bacterial autolithification and imprintation occur) the probable mechanism for this early decay inhibition was rapid/high sedimentation rates. The linking of preservational styles and sedimentary environments has been noted before and termed "Taphonomic Windows" (*sensu* Allison and Briggs, 1991). These taphonomic windows are described below.

5e1. Amber

Feathers in amber are rare because they are trapped by accident rather than being attracted to it as are insects. However, amber produces the best feather preservation. This is in part due to the antibiotic properties of the terpenes (Henwood, 1993) in the resin, and the dehydration of the keratin molecules. This taphonomic window has the potential to occur anywhere where amber deposits are found because the fossil record of birds overlaps with the time range of amber (although large amounts of amber must be processed to locate feather remains).

5e2. Coprolites

Coprolites are an unlikely mode of preserving feathers which could occur, theoretically, in any sedimentary environment but so far are only known from the Miocene Chesapeake Formation. This rarity can be explained by the following factors.

a) Coprolites that have retained their original shape and integrity and would contain bird remains are relatively rare (due to the rapid conditions needed for preservation and the very low probablity of the right sort of coprolites to occur in these conditions).

b) Marine environments where the conditions for coprolite preservation are suitable rarely have an avifauna (they are usually open marine which, in the case of Britain, for example, has only 3.5% of the recognised avifauna: Gooders, 1987), so birds are rarely incorporated into the food chain and hence represented by feathers in coprolites (Veit (1995) analysed the avian biomass of the southern Atlantic Ocean and discovered that the average was 0-1kg per km^2. This means that only a tiny fraction of this will be incorporated into the food chain and then only a tiny fraction of this will be excreted. Therefore thechance of a coprolite containing feather is small).

c) Concentration of phosphate for authigenic mineralisation may be a factor (Prévôt and Lucas, 1991). Although phosphate is released by degradation of the coprolite by bacteria, it is not known if it is produced quickly enough and in sufficient quantity (i.e. concentration) to allow the rapid preservation of the coprolite.

5e3. Imprintation

Imprintation has been observed only in the Late Jurassic Solnhofen Limestone. The mechanisms of imprintation preservation are exceptionally rare. It involves microbially driven localised diagenesis. It is believed that this style of feather preservation is unique to Solnhofen.

5e4. Bacterial Autolithification

Bacterial autolithification is not uncommon. It occurs, for example, at Messel (in a variety of soft tissues, feathers, skin: Wuttke 1983), Holzmaden (ichthyosaur "skin" traces: Martill 1987), the Permian Lower Rotliegendes of Germany (branchiosaurian amphibian soft tissues: Willems and Wuttke 1987). Lithified bacteria are evident in other feather preservational styles e.g. coprolites and occasional specimens preserved by imprintation and as carbonised traces (Martill and Frey, 1995). This taphonomic window depends upon conditions for very rapid or instantaneous preservation of bacteria.

5e5. Carbonised Trace

This is the most common form of fossil feather preservation (in terms of localities, 78% of localities have this type of preservation, Table 5.1). The reason for this "large" taphonomic window is that degradation of the feather can take place to produce an organic trace. This organic trace can then be altered to the carbonised trace that preserves the fossil feather. The process of carbonised trace preservation requires only two conditions:

1. Fine grained, well laminated sediments (ie. no bioturbation/anoxic bottom waters);
2. Decay to be allowed to proceed and then inhibited (factors such as fluctuating anoxia / sterility).

The high probability of the occurrence of such conditions (e.g. in foreland basin freshwater lake deposits) gives a wide taphonomic window for the preservation of feathers as carbonised traces.

Name	Legend to Fig. 3.10	Age	Locality	Environment	Preservation Type	References
Willerhausen	32	U. Pliocene	Grube Willerhausen, Germany	Lacustrine	Type B	Meischner and Paul 1982
Salt Lake Group	31	U. Pliocene	Salt Lake Basin, Utah, USA.	Lacustrine	Type B	Williams 1958*; pers. obs.
Upper Freshwater Molasse	30	U. Miocene	Lake Constance, Oeningen, Germany	Lacustrine	Type B	Lydekker 1891
Latah Formation	29	U. Miocene	Washington and Idaho, USA.	Lacustrine	Type B	Pardee and Bryan 1926*; Kirkham and Johnson 1929*; pers. obs.
Chesapeake Group	26	M. Miocene	Maryland, USA.	Marine	Type E	Wetmore 1943
Chalk Mountain Fm.	27	L. to M. Miocene	Bugaldie, NSW, Australia	Lacustrine	Type B	Rich and McEvey 1977; McEvey 1985
Shanwang Formation	28	L. to M. Miocene	Shanwang, Shandong Prov., China	Lacustrine	Type B	Yang and Smiley 1992
??	25	L. Miocene	Puy de Dôme, France	Lacustrine	Type B	Lydekker 1891
??	23	U. Oligocene	Cereste, France	Lacustrine	Type B	Sigé 1971; pers obs
Polierschiefer	22	U. Oligocene	Rott, Germany	Lacusrtine	Type B	Koenigswald 1989
Creede Basin	24	M. Oligocene	Colorado, USA.	Lacustrine	Type B	Wolfe and Schorn 1989*; pers. obs.
Sieblos	21	L. Oligocene	Wasserkuppe, Hesse, Germany	Lacustrine	Type B	pers comm Dr. E. Martini and Dr. P. Rothe
Dominican Amber	20	U. Eocene - L. Oligocene	Dominican Republic	Amber	Type D	Poinar 1988
Florissant Formation	19	U. Eocene - L. Oligocene	Colorado, USA.	Lacustrine	Type B	Shufeldt 1913
Bembridge Beds	18	U. Eocene	Isle of Wight, England	Lacustrine	Type B	Jarzembowski 1980
Freshwater Beds	17	L. Eocene	Bournemouth, Hants, England	Lacustrine	Type B	Lydekker 1891
Eckfelder Maar	16	L. Eocene	Eifel, Germany	Lacustrine	Type B	pers comm Dr. H. Lutz
Geiseltal	15	L. Eocene	Geisental, Germany	Swamp	Type ?	Bachofen Echt 1936; Voigt 1988
Messel	14	L. Eocene	Grube Messel, Darmstadt, Germany	Lacustrine	Type A	Schaal and Ziegler 1988
Green River Formation	13	L. Eocene	Green River Basin, USA.	Lacustrine	Type B	Shufeldt 1913; Grande 1980
Moler Clay Formation	12	Thanetian	Jutland, Denmark	Restricted Marine	Type B	Bonde 1987
Oil Shales	11	Paleocene	Taubaté, Sao Paulo State, Brasil	Lacustrine	Type B	Shufeldt 1916
Fort Union Formation	10	L. Paleocene	Glendive, Montana, USA.	Lacustrine	Type B	Brown 1962
??	9	Campanian	South Alberta, Canada	Amber	Type D	Pike 1992
Niobrara Formation	8	U. Coniacian-L. Campanian	West Kansas, USA	Marine	Type B	Williston 1896
Crato Formation	7	Aptian/Albian	Nova Olinda, Ceará, Brasil	Restricted Marine	Type B	Neto & Kellner 1988; Maisey 1992; Martill & Filgueira, 1994; Martill & Frey, 1995
Korumburra Group	6	Neocomian	Koonwarra, Australia	Lacustrine	Type B	Talent et al. 1966; Waldman 1970
Lebanese Amber	5	Neocomian	Lebanon	Amber	Type D	Schlee 1973
??	4	Neocomian	Khurilt-Ulan-Bulak, Mongolia	Lacustrine	Type B	Kurochkin 1982
Sierra del Montsec	3	Neocomian (Barremian)	Lleida, Spain	Coastal Lagoon	Type B	Ruiz 1985 and 1986
??	2	Oxfordian-Tithonian	Karatau Range, Mongolia	Lacustrine	Type B	Rautian 1978
Solnhofen Limestone	1	Tithonian	Solnhofen, Germany	Restricted Marine	Type C	Helms 1982; Bartel et al. 1991

TABLE 5.1. List of feather localities with environment, preservational style, references and legend to figures 5.11 and 5.14. * Indicates reference to geology and palaeontology of locality only, and does not refer to the feather material.

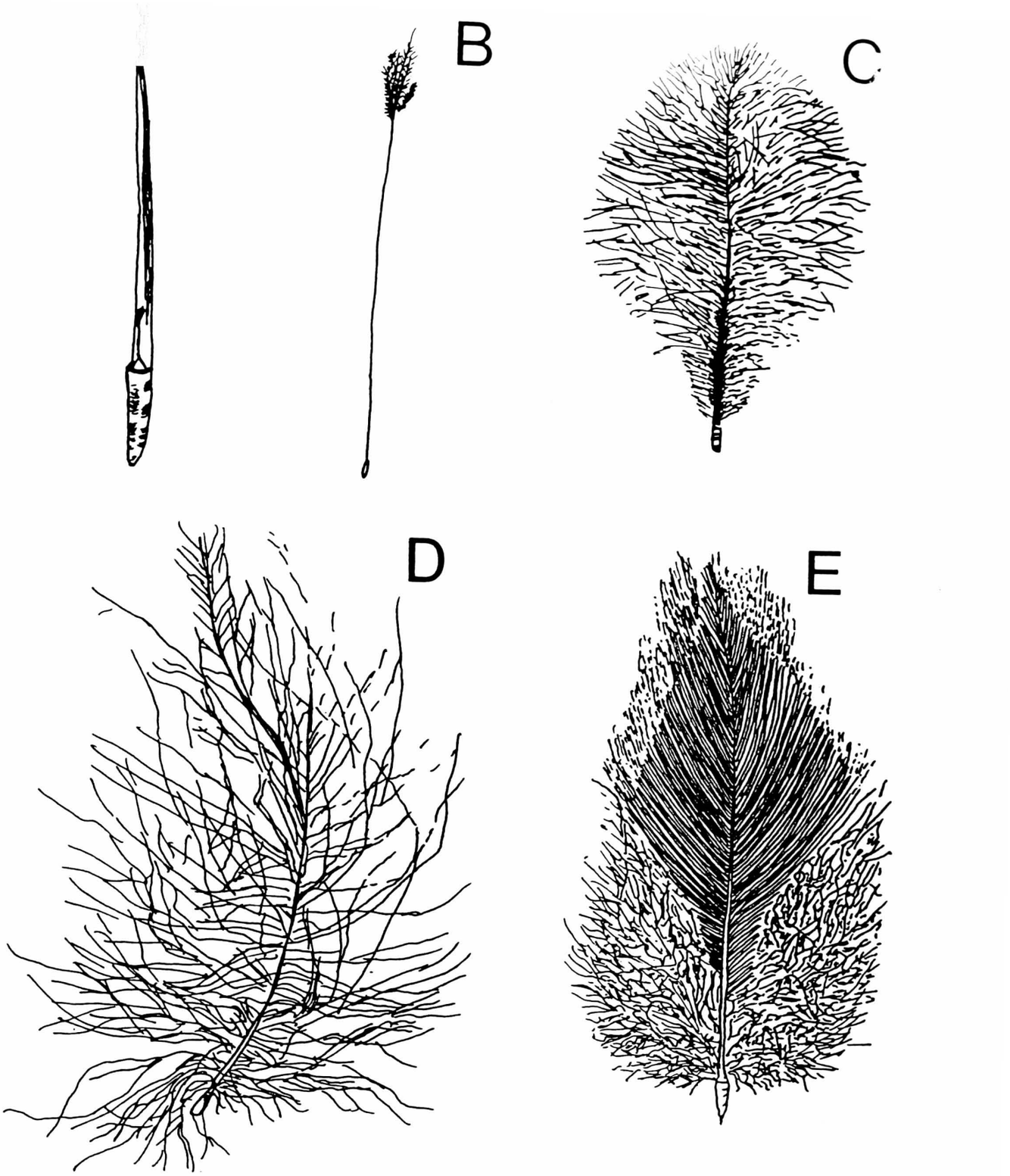


FIGURE 5.1 The five categories of feathers.

A. Bristle (x10)
B. Filoplume (x10)
C. Semiplume (x2)
D. Down (x3)
E. Contour (body) (x2)

FIGURE 5.2 An unidentified bird (HLMD Me 9047) from Grube Messel (Eocene). The central contour feather of the tail shows light and dark banding corresponding to the possible original pigmentation variation in the feather.

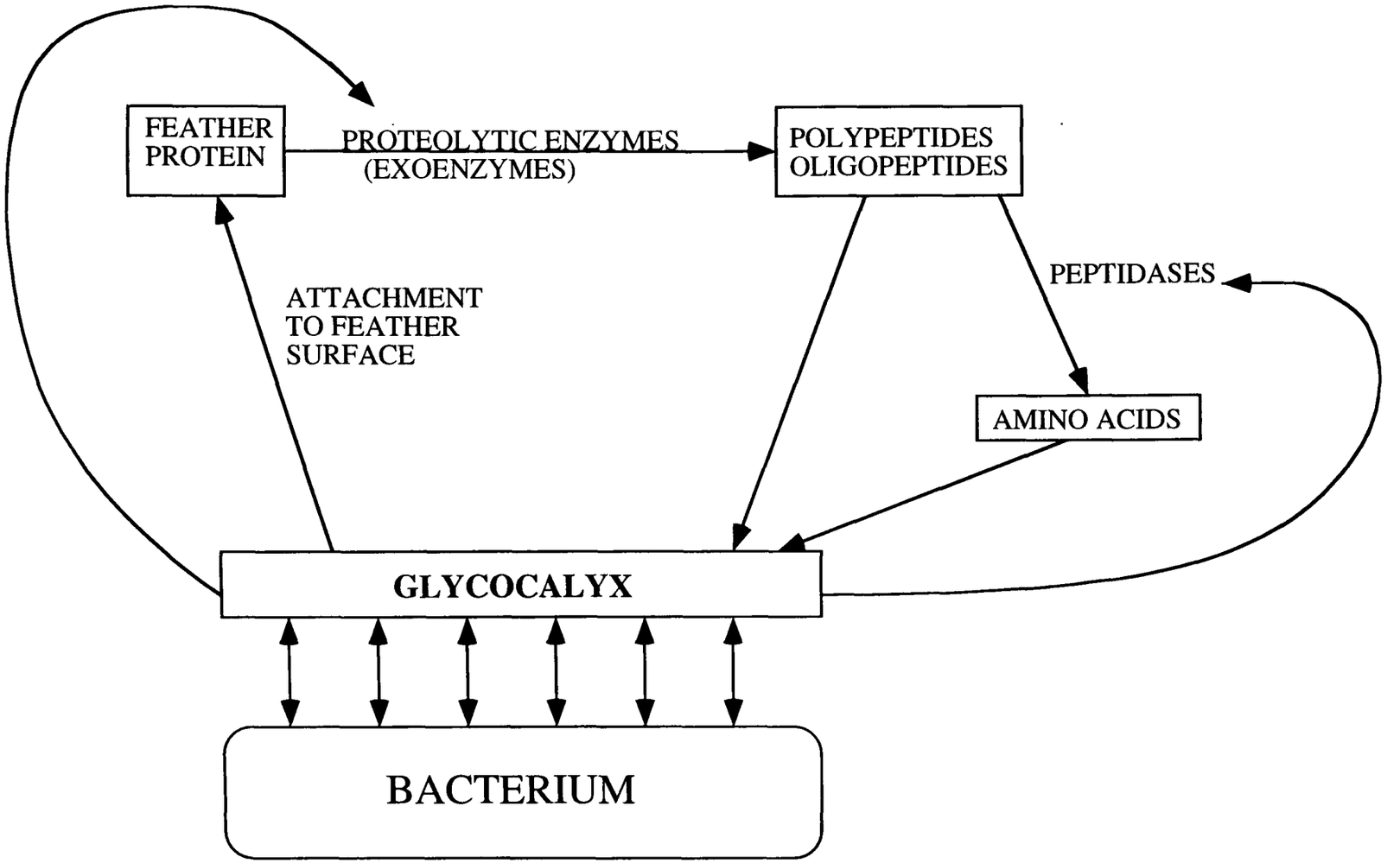


FIGURE 5.3 **Diagramatic representation of the relationship between bacteria, glycocalyx, enzymes and nutrients when attached to feather proteins.**

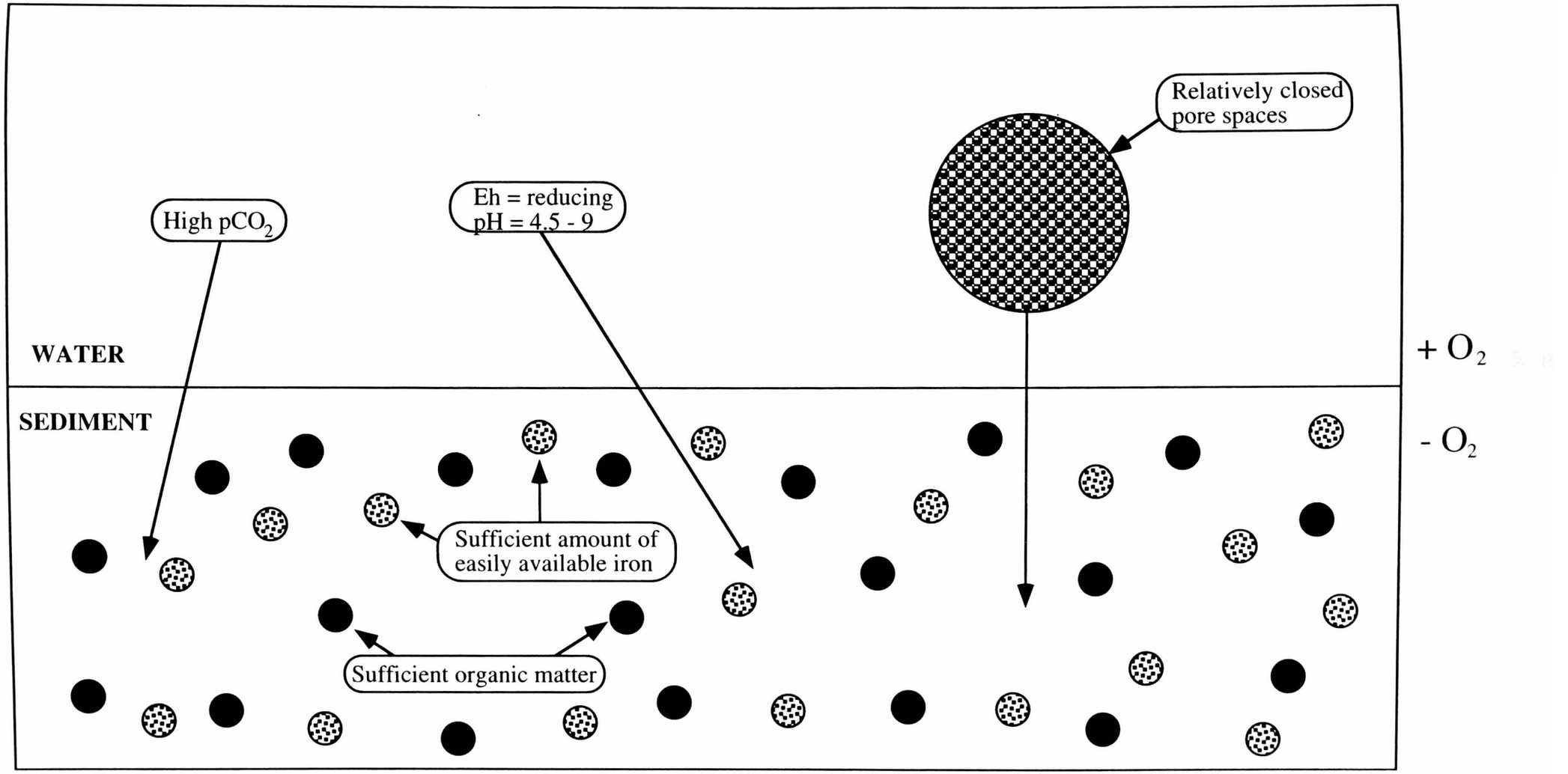
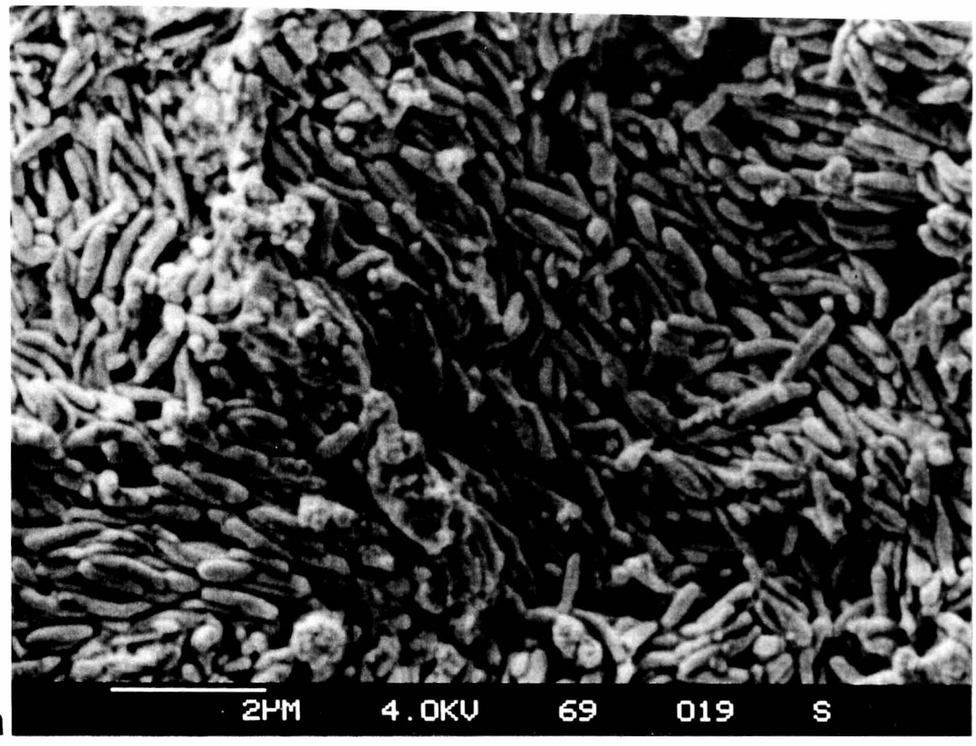


FIGURE 5.4. Constraints of siderite lithification (after Wuttke 1983).

FIGURE 5.5

A feather from Grube Messel (HLMD Me 7268b) showing bacteria replicating the shape. The top photograph (a) shows the bacteria in a "flowing mat" structure. This is caused by the arrangement of bacteria which insured maximum bacterial contact with the feather. The bottom photograph (b) shows the delineation of a vane by the bacteria. The bacteria have only colonised the original feather material.



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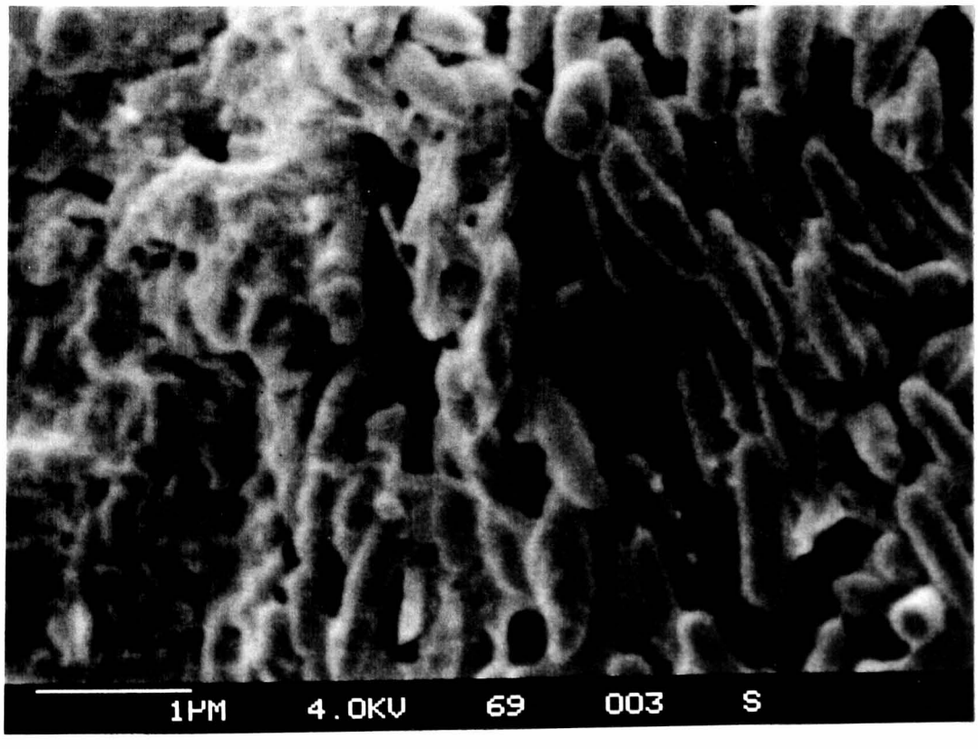
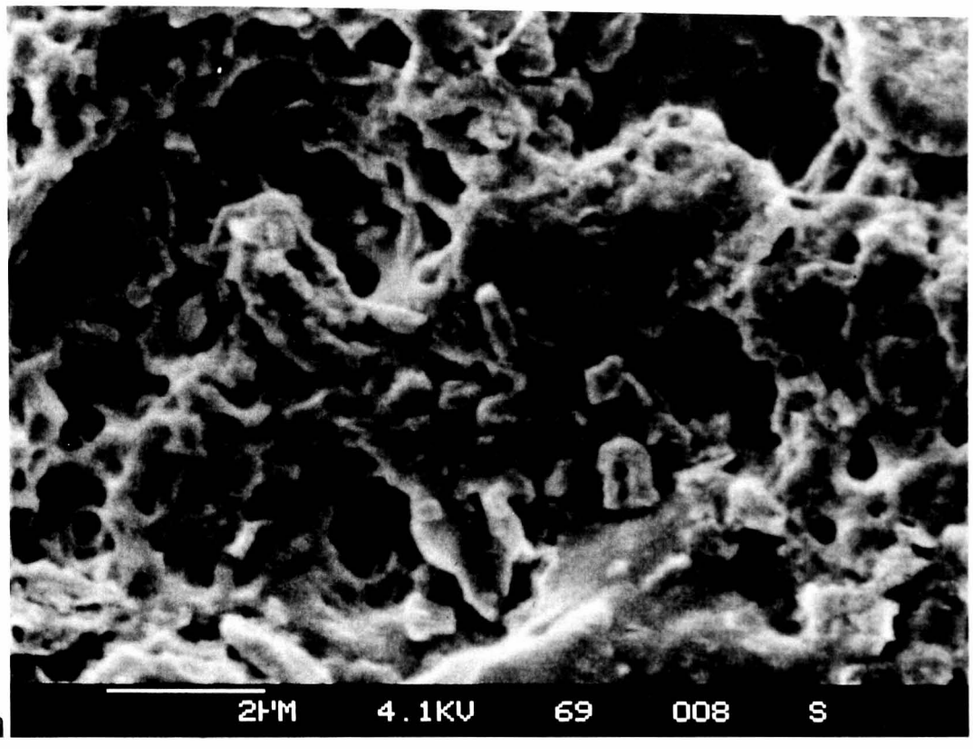


b

FIGURE 5.6 The honeycomb texture of fossilised bacterial glycocalyx. The lower photograph (b) shows irregular rod shaped structures that may be lithified bacteria. Their shape may be the result of recrystallisation of the preserving mineral (probably calcite). The specimen is a contour feather from the Oligocene of Cereste (France).



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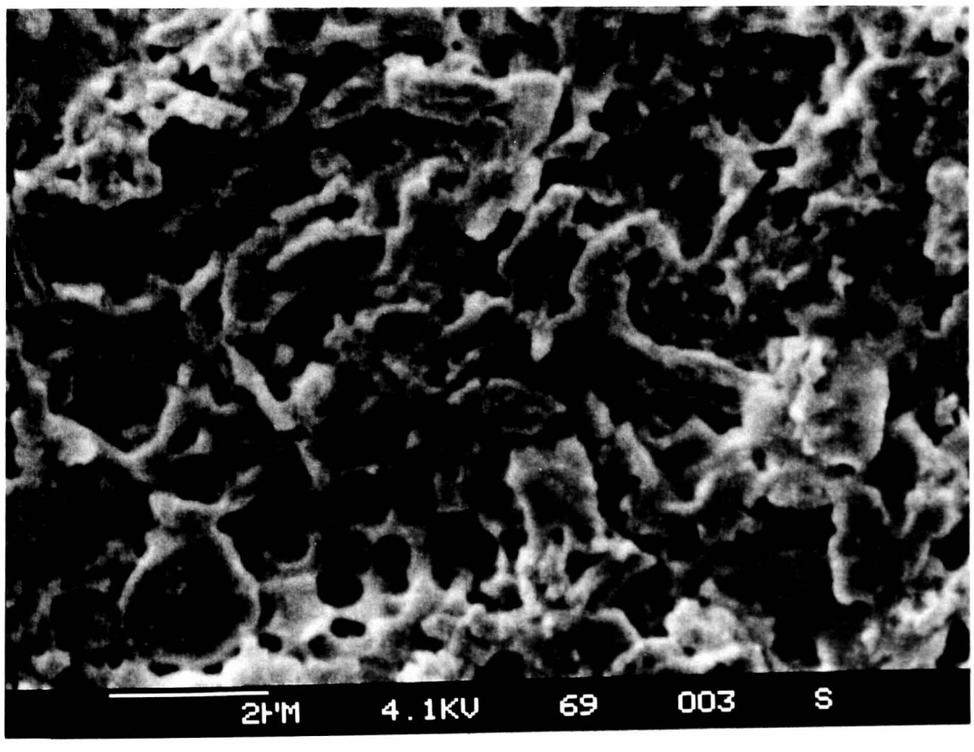

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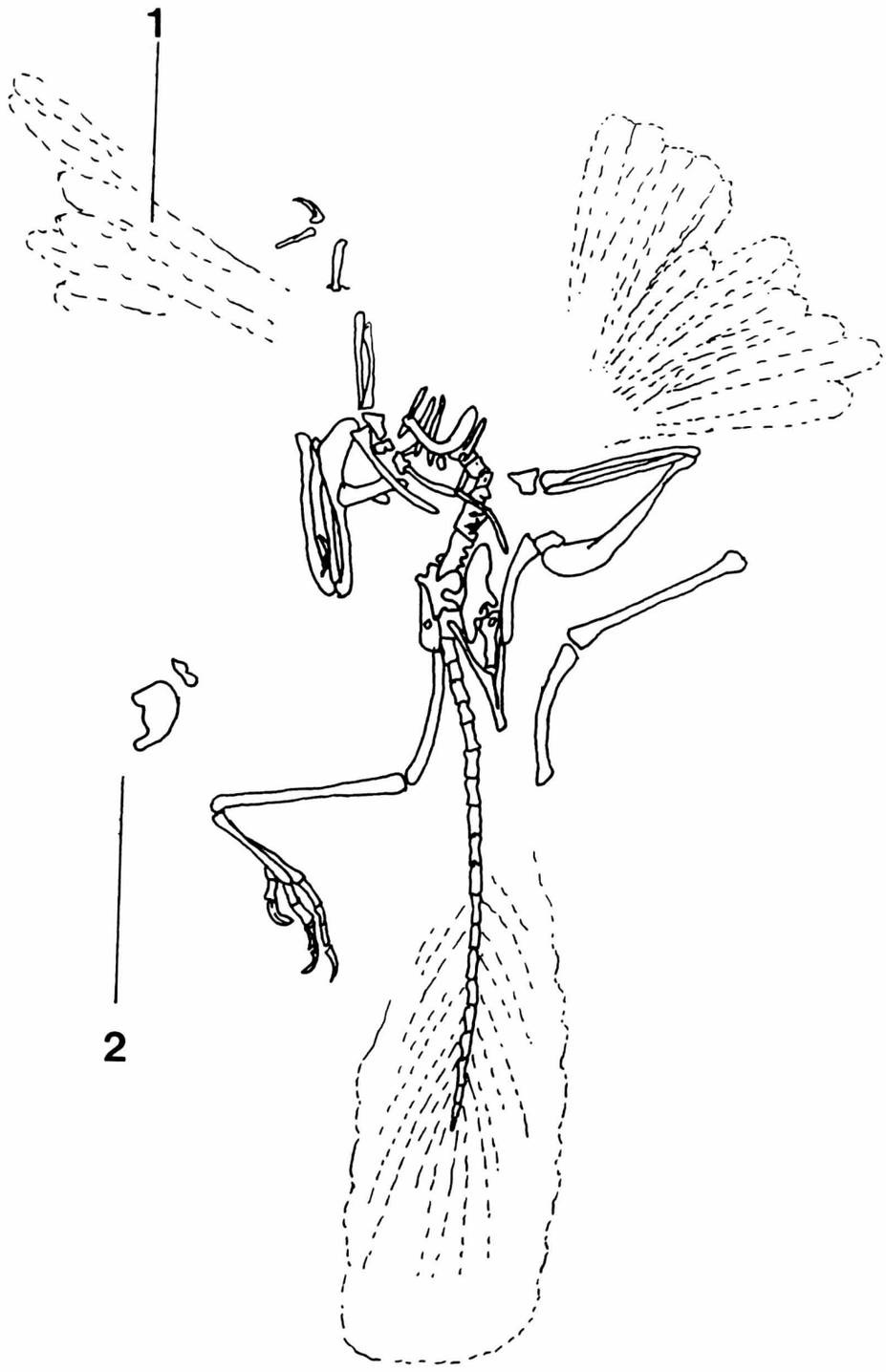
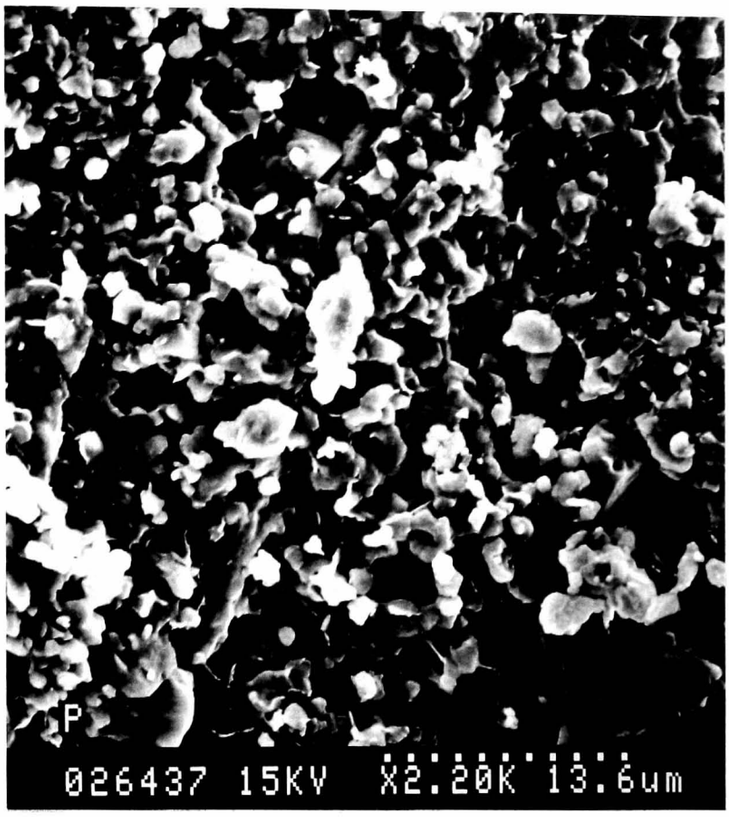


FIGURE 5.7 Diagram of the London Archaeopteryx specimen (BMNH 37001) showing the localities of the two samples removed for SEM analysis. Sample 1 was removed from the counter slab in the region of the 3rd or 4th primary wing contour feather. Sample 2 was removed from the region of the braincase. Figure is half lifesize (x0.5).

FIGURE 5.8

Matrix (sample 2) of the London *Archaeopteryx* (BMNH 37001), for comparison with Figure 5.9. The top photograph (a) shows clay particles (flat sheets) and carbonate grains (cuboid crystals). The bottom photograph (b) shows a higher magnification of the carbonate grains showing that in places the limestone is exceptionally pure. The sample was taken from the main slab in the region of the braincase.



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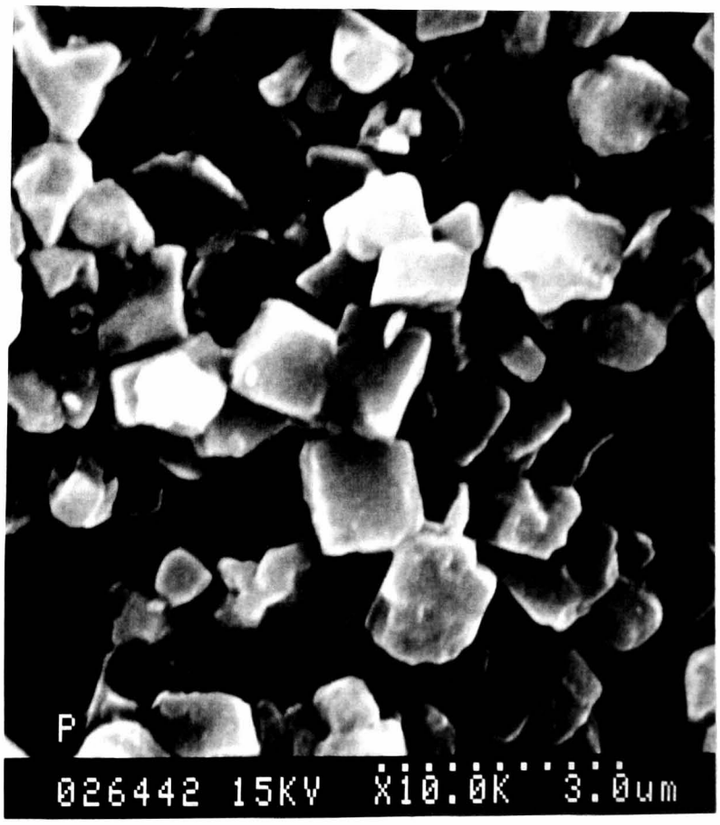


b

FIGURE 5.9

Feathers of the London *Archaeopteryx* (BMNH 37001). The top photograph (a) shows a flowing mat of bacteria, in which individual bacilliform bacteria are evident. The smooth texture is caused by preservatives applied to the specimen. The bottom photograph (b) shows an individual bacilliform bacteria. The irregular shape is caused by the gross form of the preserving mineral (possibly carbonate). The smooth texture is caused by preservatives applied to the specimen.

a

b

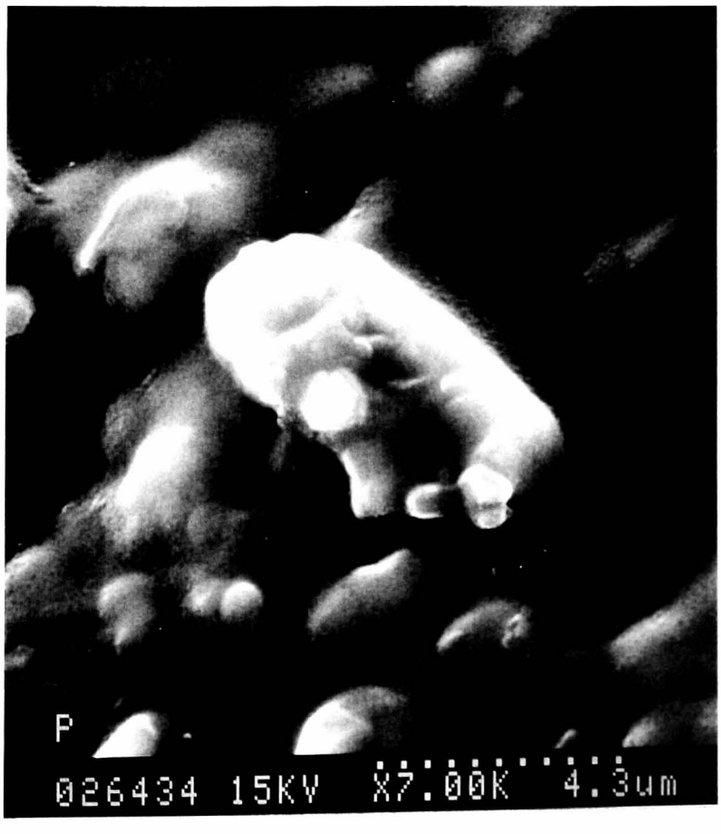
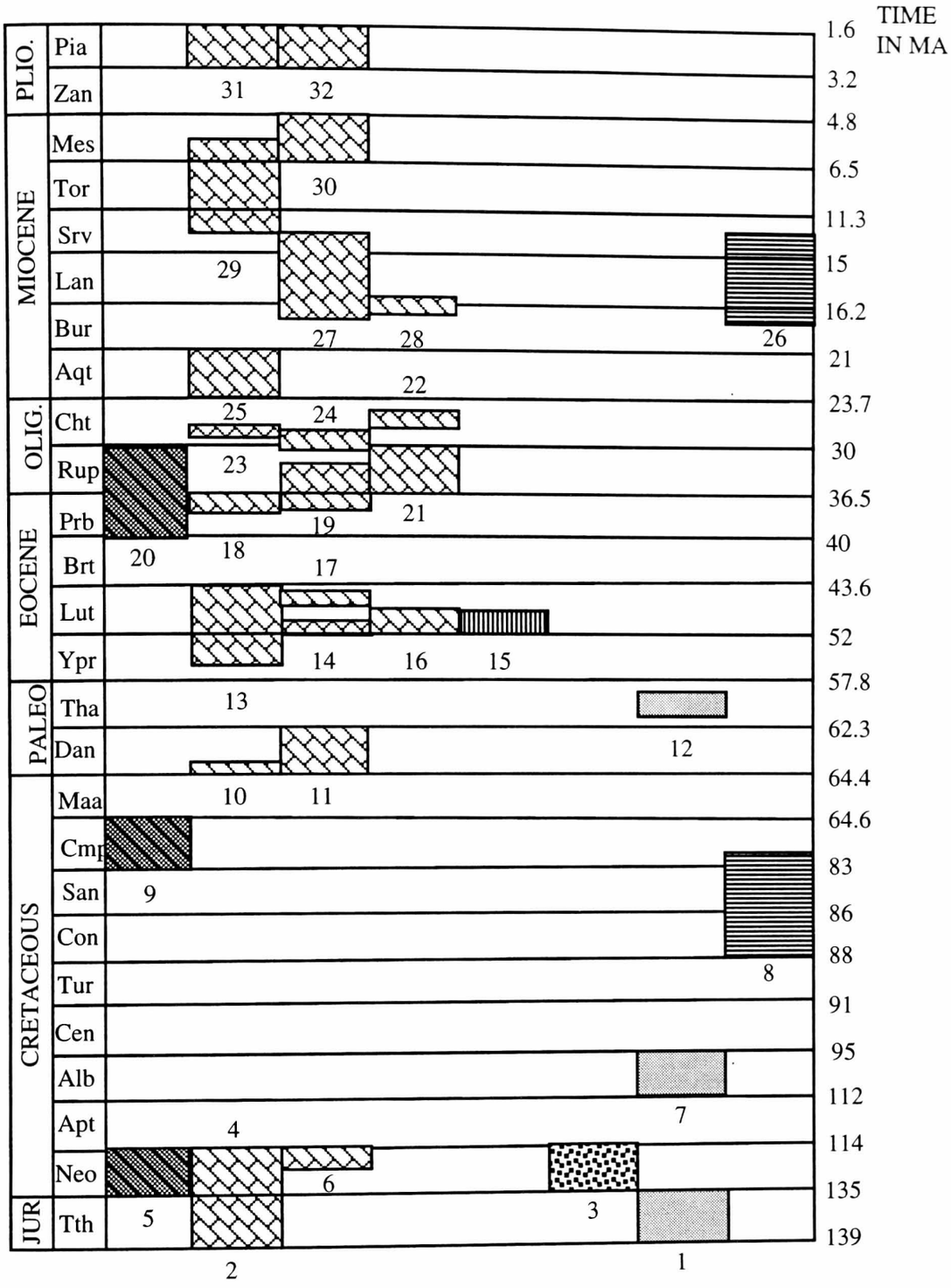


FIGURE 5.10 A down feather preserved in amber. The feather is perfectly preserved and shows the inter barb nodes. This specimen is from the Cretaceous Foremost Formation, Alberta, Canada. This photograph was taken and kindly donated by Dr. Ted Pike.



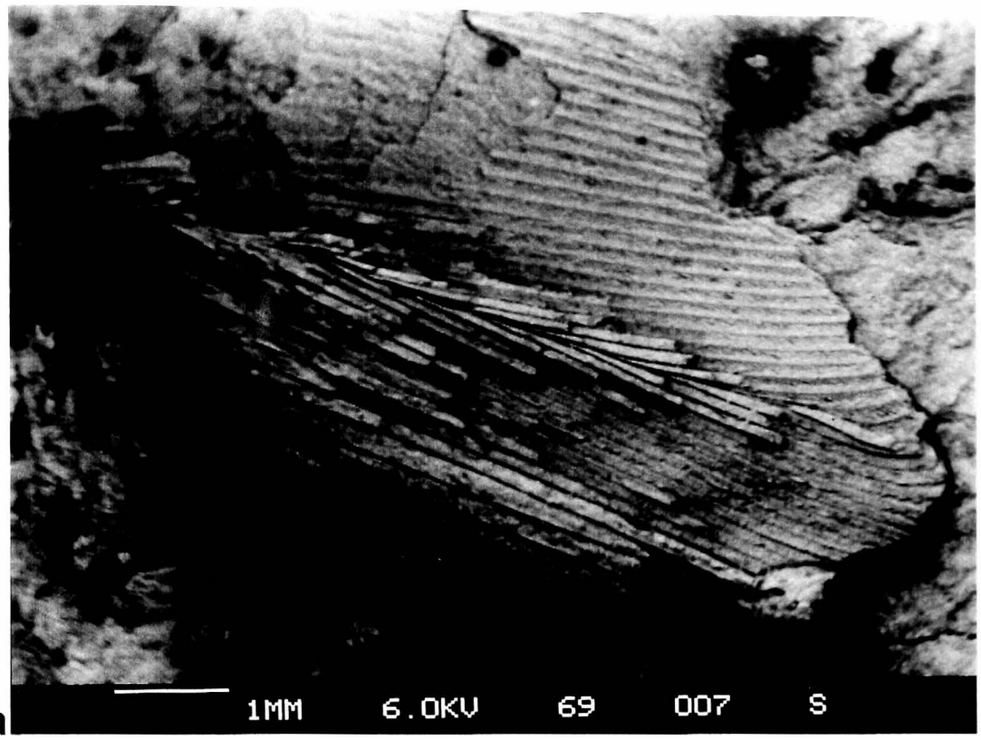
LEGEND

- Amber
- Lacustrine
- Swamp
- Coastal Lagoon/Flats
- Restricted Marine
- Marine

FIGURE 5.11
Feather localities plotted against time and placed into sedimentary environment categories.

For Legend for numbers 1 to 32 see Table 5.1

FIGURE 5.12 A body contour feather preserved as an external mould within a fossilised coprolite (USNM 16738) from the Miocene, Chesapeake Formation. The top photograph (a) shows the complete feather. The bottom photograph (b) shows the fine detail retained by the impression. The rachis can be seen in the bottom left of the photograph. Radiating from this are the vanes of the feather. Between the vanes of the feather the individual barbs can be observed.



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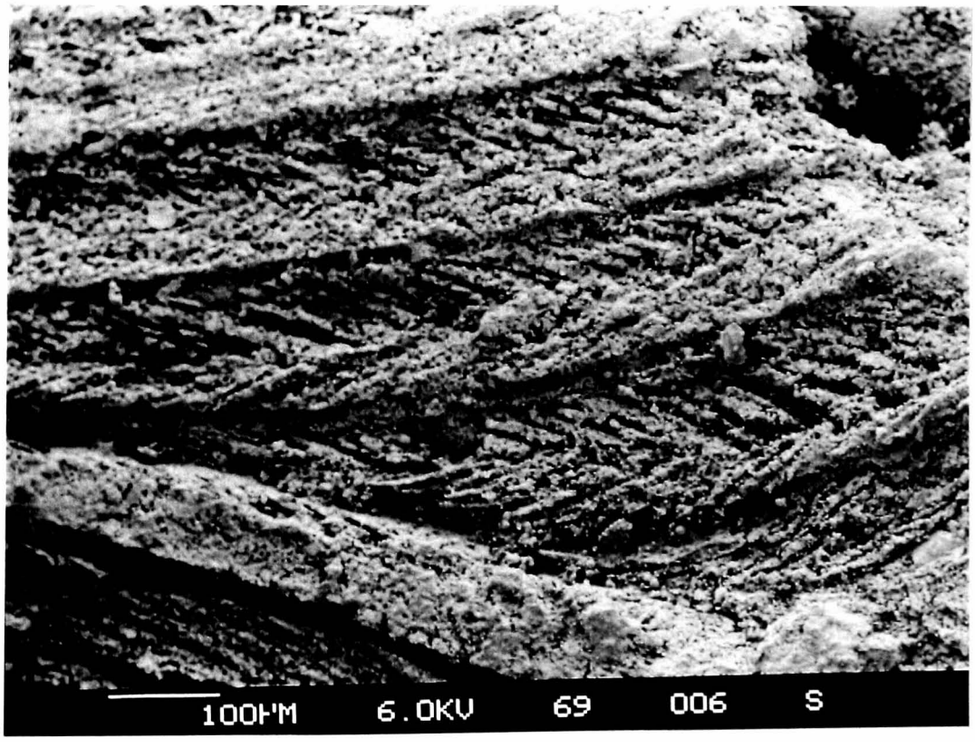
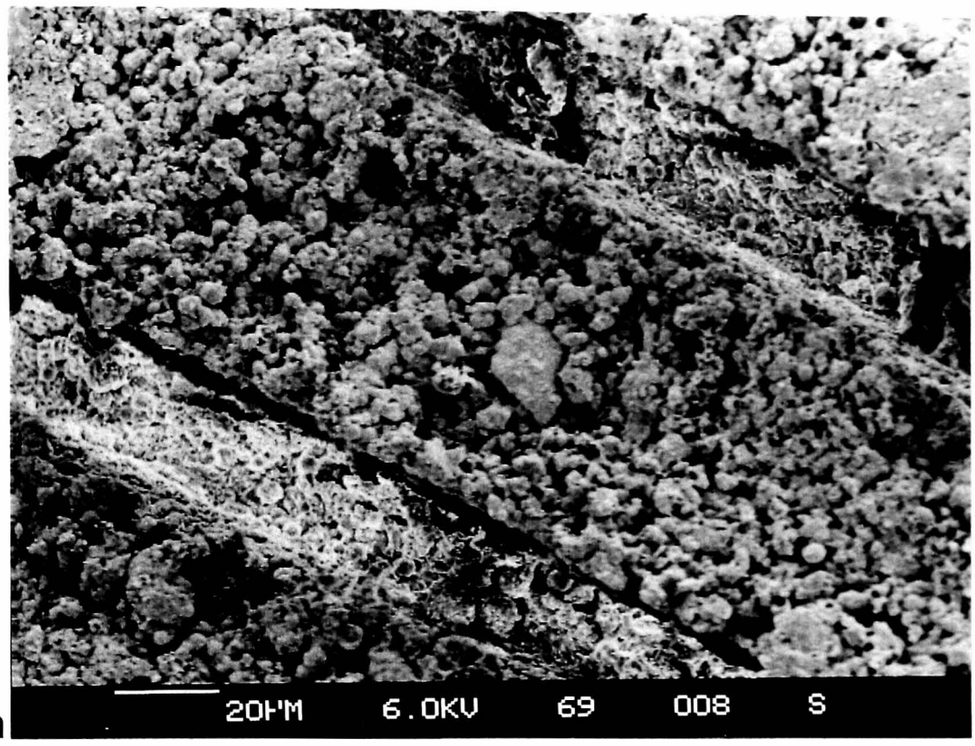


b

FIGURE 5.13 Feather in a coprolite (USNM 16738) from the Miocene, Chesapeake Formation. The top photograph (a) shows the very fine impressions of two barbs within the coprolite. The sediment in these regions show differential compaction. The bottom photograph (b) show phosphatised bacterial spheres within the coprolite.



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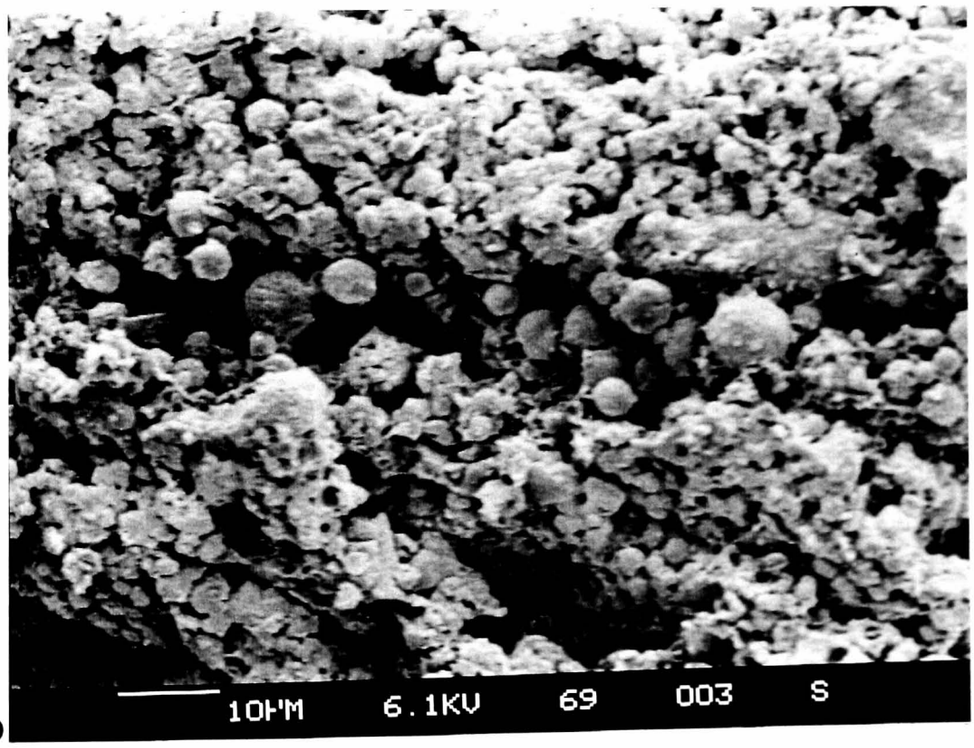
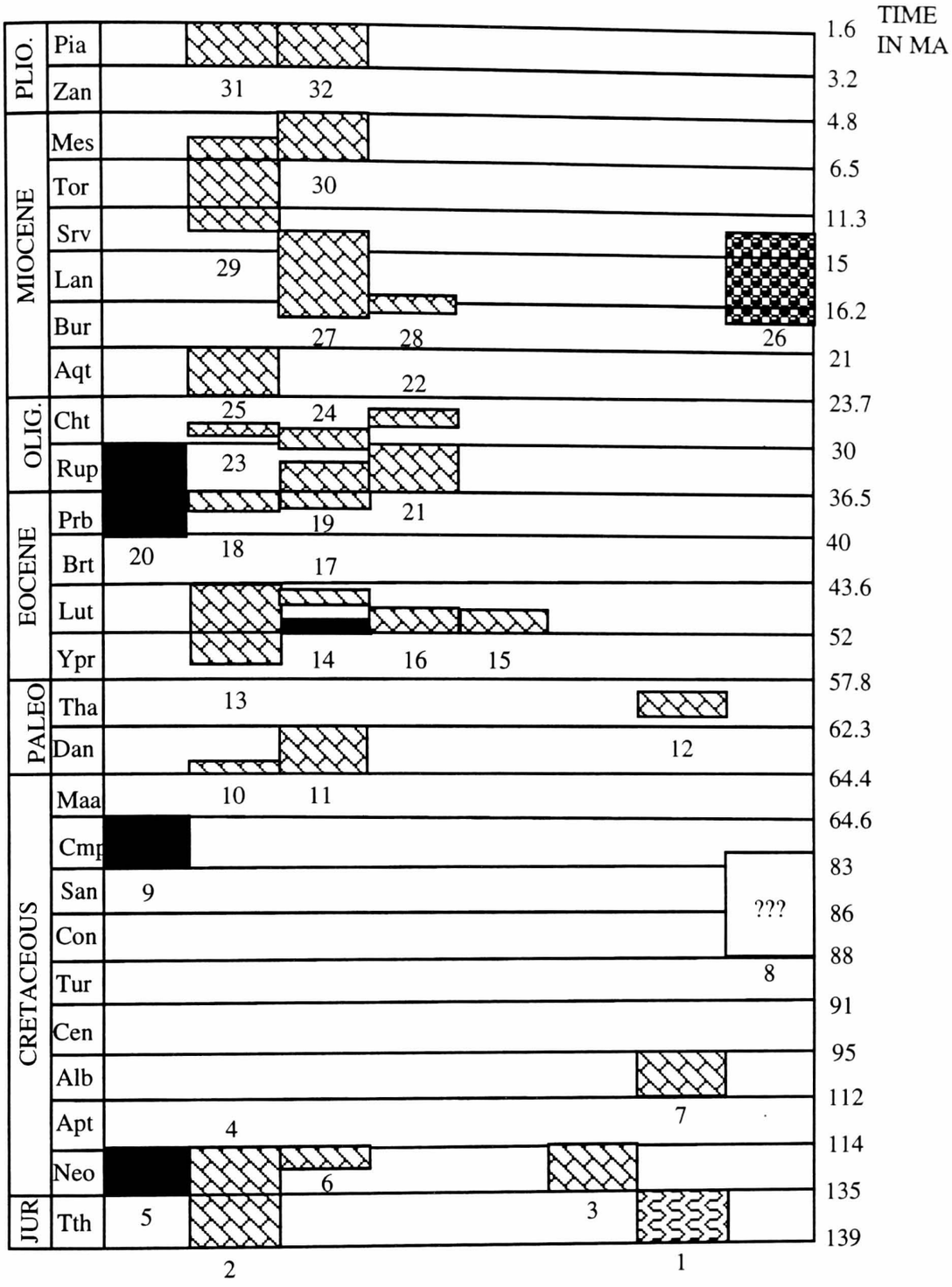


b



LEGEND

Type A: Bacterial Autolithification

Type B: Carbonised Trace

Type C: Imprintation

Type D: In Amber

Type E: In Coprolites

FIGURE 5.14
Feather localities plotted against time and placed into preservational style categories.

For Legend for numbers 1 to 32 see Table 5.1

Chapter Six
Case Histories

6a. Introduction

Previous chapters have dealt mainly with the actualistic taphonomy of birds in modern environments. The application of these data to case histories from the fossil record allows the analysis and interpretation of these fossil environments in terms of modern biological systems. It rapidly becomes apparent that "comparative taphonomy" must form an integral part of any palaeo-ecological study.

The five case histories (selected from the most significant bird deposits, Table 1.1), Messel, Green River, Solnhofen, Seymour Island and Rancho La Brea were chosen because:

a) They cover the spectrum of Lagerstätten in which avian remains are found. Thus they allow the influence of different sedimentological environments (i.e. lacustrine, restricted lacustrine, marine, restricted marine, and terrestrial "trap") upon the taphonomy of birds to be compared. Fully terrestrial and fluviatile environments are absent from this list because, with the exception of amber (a special case) avian remains are rarely preserved in these settings.

b) They all contain large numbers of specimens, allowing statistically based comparisons (except Solnhofen, where the complete sample size is only seven).

c) The geology and palaeontology of these localities has been well researched, providing a sound platform for the investigation of avian taphonomy.

Birds are represented in the fossil record in a sequence from complete skeletons with soft tissues and feathers to isolated, damaged bones. It is possible from the study of Konservat and Konzentrat Lagerstätten to identify a series of points corresponding to the qualitative experimental sequence of decay stages previously defined (Chapter 2b4.). These stages were identified in the fossil specimens by assessing the maximum stage of morphological decay represented. These data on fossil birds were obtained by extensive surveys of worldwide museum collections (Appendix 5) containing all known fossil material for Green River (see Chapter 6c), Solnhofen (see Chapter 6d), and Seymour Island (see Chapter 6e) and also the complete fossil bird collections of the Hessiches Landesmuseum, Darmstädt to study a large proportion of the material obtained from Grube Messel (see Chapter 6b). These surveys took the form of photographing

every individual specimen and completing a *pro forma* (Appendix 6) summarising the taphonomic data e.g. lithology, deformation, death marks, landing marks, preservation of soft tissues and feathers, morphological decay stage, phosphatisation.

Identification of decay stages

It was observed in the fossil specimens that the morphological decay stages overlap (as reported in the results of the decay experiments, Chapter 2b4.) and not every specimen follows the sequence exactly. Thus a specimen that is intact, except that the pectoral girdle has disarticulated, is placed in stage 3.c, even though it appears to have "bypassed" stages 3.a and 3.b (Figure 6.1). The following sequence, defined on the basis of the experiments, can be identified in fossils from the Green River, Grube Messel, Solnhofen Lithographic Limestone and Seymour Island Lagerstätten (Table 6.1). These four Lagerstätten were used because they provide the most complete samples available for analysis (Chapters 6b to f).

1. Complete skeletons with soft tissues and feathers (Figure 6.2).

   The occurrence of specimens in this condition is rare (Table 6.1). Their rarity is due to the rapidity with which the specimen needs to be preserved to show soft tissues and feathers. Soft tissues decay rapidly (Chapter 2b6.) and for a specimen to show these tissues the conditions of preservation must arrest decay and disarticulation soon after death.

2. Complete skeleton without soft tissues or feathers (Figure 6.3).

   The majority of complete specimens within Lagerstätten fall into this category (Table 6.1). The lack of soft-tissues or feathers combined with a well preserved skeleton indicates that one of two possibilities occurred to create these conditions. Either decay proceeds long enough to degrade the soft tissues and feathers before fossilisation takes place, or, the carcass is buried complete with soft-tissues and feathers but conditions are not conducive to their preservation.

3. Skeleton partially disarticulated (Figures 6.4, 6.5 and 6.6).

   The majority of avian remains from Konservat Lagerstätten can be placed within this category (Table 6.1). Fossils can be found which match the morphological decay subdivisions (3.a to 3.g). These stages represent varying times of cessation of decay and disarticulation.

4 and 5. Skeleton totally disarticulated (Figure 6.7).

   This is the most common mode of preservation of avian remains. It ranges from disarticulated skeletons in which all the individual elements are located in a small area (morphological decay stage 4) to scattered individual, isolated bones (morphological decay stage 5). This range

can be explained by differing sedimentological regimes, e.g. single bones are likely to occur more frequently in high energy sedimentological systems whereas disarticulated but complete specimens require very low energy sedimentological regimes. It must be noted, however, that high rates of sedimentation and consequent rapid burial may allow the preservation of articulated skeletons even in high energy sedimentological systems.

The data from Table 6.1 indicate that the Solnhofen Lithographic Limestone contains the "best" preserved fossil birds (71% of specimens in morphological decay stages 1 and 2), but it must be remembered that only seven specimens have been recovered.

The data from the other three Lagerstätten reflect the fact that Green River and Messel are Konservat Lagerstätten (*sensu* Seilacher *et al.*, 1985) and that Seymour Island is a Konzentrat Lagerstatte (*sensu* Seilacher *et al.*, 1985). This is evidenced by the fact that Green River and Messel contain high proportions of fossil specimens within categories 1 to 3.d (86% for Green River and 93% for Messel) whereas Seymour Island contains 0% in the same categories, but 100% in categories 3.e to 5 (whereas Green River and Messel contain 14% and 7% respectively).

These data therefore indicate in which environment the inhibitors of decay and disarticulation were most effective i.e. it is a measure of the "quality" of a Lagerstatte. Obviously the "quality" of a Lagerstatte cannot be assessed by just one class of organisms. So by completing similar experiments for a range of organisms and then comparing these results it would be possible to produce a Lagerstatte "quality index".

Factors Inhibiting Decay in Lagerstätten

The morphological decay sequence reflects factors that enhance decay and disarticulation. It can therefore be used to deduce what will inhibit them. The following factors are required for a high grade of preservation.

1. Anoxia

   Anoxia inhibits decay by preventing the microbial aerobic decay of organic carbon. Anaerobic microbial decay will continue to operate, although in conjunction with other limiting factors (such as low temperatures) it too may be inhibited (Allison and Briggs, 1991). The perfect preservation of the birds of the Eocene Grube Messel Lagerstatte is in part due to the anoxic properties of the benthic water (Schaal, 1992).

2. Transport

Transport increases disarticulation, therefore low energy sedimentological regimes are required (or rapid burial, see point 4 below). Both sets of protected specimen experiments (FLP, FSP, SLP, SSP, Table 2.3) were carried out in low energy environments. Therefore the only disarticulation that occurred was decay-induced. This allowed the decay sequences to be studied without the added complications of transport effects. It can be assumed that disarticulation caused by transport will follow a similar pathway to those already observed, because protruding elements such as the head/neck, wings, and legs will be removed first. The torso remains protected from transport induced disarticulation by soft tisues. Therefore once soft tissue decay has occurred the torso will also become disarticulated (and again a direct comparison of the decay stages described in Chapter 2b4. can be made). The Eocene La Meseta Formation of Seymour Island, Antarctic is characterised by wave and tide dominated sedimentation. The birds in this deposit have been subjected to transport. This is evident in the skeletal specimens which are always found disarticulated, with a high proportion of broken bones (Chapter 6e).

3. Scavenging

Scavenging has been shown to increase the rate of weight loss. In environments where scavengers are inhibited e.g. hypersaline lagoons, deep marine, carcasses will remain intact longer and therefore have a greater chance of preservation. It must be remembered that other factors such as rate of burial can reduce the effect of scavenging. The Solnhofen Limestone Lagerstatte shows no evidence of scavenging due to the hypersaline condition of the lagoon during time of deposition (Barthel *et al.*, 1990), which contributed to the excellent preservation of *Archaeopteryx*.

4. Rate of Burial

Rapid rate of burial influences decay and disarticulation in a number of ways. It can stop scavenging, it can create anoxic conditions, and it can also stop transport. The experiments in marine conditions involved a rapid rate of burial. The observed effects of this were to keep the skeletal elements together after disarticulation, to prevent scavenging by the crown conch (*Melongena corona*), and to create anoxic conditions (anaerobic decay processes persisted and after 70 days iron monosulphides were deposited in the small bones of the ovenbirds - see Chapter 2b5.). The Eocene Green River Formation Lagerstatte had periodic high sedimentation rates (Grande, 1984) and this allowed, at certain times, the

rapid burial of bird carcasses. This created an environment which led to the exceptional preservation of some of these carcasses.

5. Temperature

   Temperature affects the rate of decay (Chapter 2b6.). The relationship between the two is simple, for every increase in temperature of 10°C the rate of decay doubles and conversely halves for every decrease by 10°C (Swift *et al.*, 1979).

6b. Restricted Lacustrine Environment: Grube Messel

6b1. Introduction

In 1875 an open cast mine was opened near the town of Messel, near Frankfurt, Germany. The reason for the mine was to excavate 'Braunkohle' or oil shale (Schaal and Ziegler, 1992). On the 30th December 1875 the first fossil was recovered (a partial crocodile) by R. Ludwig from these middle Eocene (Lutetian) sediments (Schaal and Ziegler, 1992). Since then hundreds of thousands of fossil specimens (representing a diverse ecosystem) have been excavated from this unusual locality.

6b2. Study Methods

The complete collection (124 specimens) of Messel birds in the Hessiches Landesmuseum, Darmstadt were reviewed for this study. This review took the form of photographing and making taphonomic observations upon every specimen, this involved recording the amount and type of disarticulation (later summarised into the decay stages described in chapter 2), e.g. presence/type of soft tissues, compaction, diagenesis. The data for each specimen was recorded on a *pro forma* (Appendix 6) and then summarised (Appendix 8). The Landesmuseum collections were chosen for survey because they contain a significant proportion of all the fossil bird specimens recovered from the site. All specimens are collected (irrespective of quality) and transferred to the collection (i.e. no collection bias).

6b3. Sedimentology and Palaeo-Environment

The formation of this deposit is due to the underlying structure of the Messel graben (see Schaal, 1992 Figure 4, p. 19). This graben was active during Eocene times, allowing an extended period of sedimentation to occur within the Messel region.

The sediments at Messel consist of oil-shales. These oil-shales have been subdivided into four facies (Franzen *et al.*, 1982; Goth, 1986). Colouration of the shales, and the presence of siderite or phosphate (neomesselite, montgomeryite) (Schaal, 1992), are the main factors distinguishing these facies. Three aspects of the genesis of these deposits require explanation:

1. The stratification of the oil shale.
2. The abundance and diversity of the flora and fauna.
3. The state of preservation of the fossils.

This last point is the only one that has been satisfactorily resolved. According to Schaal (1992) the state of preservation of the fossils is due to the subtropical to tropical climatic conditions which resulted in high algal production. The decay of the algae in the lower water layers created an anoxic environment. This anoxic environment led to incomplete decomposition of the organic matter but more important palaeontologically, provided conditions which allowed the fossils to remain almost intact. This is a simplification of the complex taphonomy of the Messel fossils.

Three models have been proposed to explain the stratification of the oil shale and the abundance and diversity of the fauna/flora. The first model envisages a basin within an extensive river system. This was proposed by Franzen *et al.* (1982) who suggested that the Messel region was an essentially flat landscape through which flowed a large river of unknown direction and extent. During Eocene regional tectonic activity the Messel graben became active. This caused a local depression which interrupted the passage of the river by creating a lake. Lake Messel was, in effect, a basin into which plant debris and animal corpses drifted and accumulated. The area was sinking tectonically, which delayed the silting up of Lake Messel. The lake was judged to be approximately a few square kilometres in area (about the size of the present day opencast mine at Messel) and in the quiet still portions of the lake the suspended load (clays/silt) of the river was deposited along with its cargo of animal and plant remains. Directional measurements were taken on the numerous remains of fish and caddis fly larvae from excavations carried out over several years. The results of this analysis allowed Franzen *et al.* (1982) to reconstruct palaeo-currents in the lake and also determine the position of two entering tributaries and the river outlet from the lake (see Figure 6.8).

Schaal (1992) proposed a second model, that the Lake Messel sediments preserved represent a small section of a large lake. He stated that detailed recording of profiles show homogeneously formed layers across large areas of the site. The graben acted as a sediment trap for clay particles which spread as clouds of mud over large areas in the lake, especially at times of increased water levels. The dead plants and animals drifted in this water and settled out together with the clay particles. Schaal (1992) used evidence from Reineck and Weber (1983) to argue the presence of a distinct trough. Thus, although Lake Messel is assumed to have changed in volume and extent frequently, the graben never dried out and the lake could have served as a refuge for aquatic life in times of drought. Further evidence is derived from the chemical and biochemical reactions particularly at the lake bottom, which would have been drastically influenced by these water level

oscillations and are mirrored by the corresponding precipitation of minerals (Schaal, 1992). This model also explains the abundance of fossilised aquatic animals as these would have inhabited the lake at all times. In contrast, preservation of the terrestrial flora and fauna is more subject to chance, the frequency of finds is relatively small, and they occur just as often at the lake borders as at the centre of the site.

Rietschel (1987) proposed a third model which explains the Messel graben as a maar-like crater of volcanotectonic origin. He considered the anomalies in the flora and fauna present (such as the absence of crustaceans, water insects, water birds, herbivorous fish and lake border vegetation) and reached the following conclusions. After major subsidence the crater filled up with coarse decaying debris and water until a surface outlet could be formed, so that a deep lake with steep sides and predominantly hostile environmental conditions became established within a subtropical forest. Fishes and reptiles were able to reach the lake via the lake outlets, and springs providing groundwater input to the lake sustained the freshwater fauna. Small streams carried a light clay suspension, which was deposited in the lake together with flowers and leaves blown into the water and with mammals that fell into the lake along its borders.

This model can be used to explain certain absences in the fauna including, for example, water insects and water birds. Between the primary producers (green algae) and carnivorous fish, herbivorous fish are absent. In addition there are floristic absences such as roots, stems, branches and twigs. Furthermore, besides water-lilies, the higher water plants and representatives of vegetation from the border of the lake are missing. Rietschel assumed that the good fossil preservation could also be due to the presence of gases with conserving properties, which might even have contributed to the death of the animals.

6b4. Palaeo-ornithology and Faunal biasing

Peters (1992) presented a faunal list (Table 6.2) for the Messel deposits. He noted that this survey was not complete because only specimens that could be safely placed into the systematic framework were included. A similar modern environment such as the neotropical rain forest of South America contains up to 38 bird families (after passerine families have been removed) (Welty and Baptista, 1988). Thus the Grube Messel avifauna which only contains 18 families, is clearly depauperate (by comparison with a modern environment). True water birds (with the possible exception of *Juncitarsus merkeli*, Family Phoenicopteridae) are absent which is anomalous considering that the deposits at Messel are supposedly those of a standing

body of water. *Juncitarsus merkeli* is only known from one specimen; therefore it was not frequent at the lake (assuming that fossil abundance can be translated into real biological abundance). This observation is consistent with other evidence that the lake was not at times a welcoming body of water to aquatic organisms.

Wading birds (Messelornithidae and Plataleidae) are the most numerous (93% of specimens, n=124) in the assemblage and this indicates that the habitat surrounding Lake Messel was moist and not hostile (in comparison to the actual standing body of water). The abundance of wading birds is predictable as their habitat would have been close to the lake and they did not require lengthy transport to be incorporated within the lake sediments.

The remaining avifauna consists of terrestrial birds (Palaeotididae, Diatrymidae, Phorusrhacidae, Cariamidae, Caprimulgiformes, Atelornithidae), flying predatory birds (Accipitridae, Palaeoglaucidae), flying insectivorous birds (Aegialornithidae) and arboreal birds (Coraciidae and Capitonidae). This assemblage appears to contain a diverse selection of families that would inhabit the area around a tropical lake, e.g. the Aegialornithidae would feed on insects over and around the lake. There is a high proportion of terrestrial predatory birds and this may reflect the rich associated mammal fauna on which these birds probably fed.

6b5. Discussion

Cause of Death

The cause of death can never be totally ascertained. Rietschel (1987) suggested that the death of the birds was due to poisonous gas escaping from the lake bed while they were flying over. However, some will have died by 'normal' modes of death (such as those proposed by Shipman, 1981: predation, disease, senility, accident and starvation/dehydration).

Biostratinomy

If Rietschel's (1987) hypothesis is assumed to be correct only in part, then all the birds did not just "fall into the lake" (because they were poisoned by gases) whilst flying over it. The incorporation of these birds into the lake sediments must then be explained. Schaal's (1992) hypothesis provides a possible explanation. He implies that there were two inlets into Lake Messel (Figure 6.8), thus providing a mode of depositing carcasses in the lake.

If a proportion of bird carcasses were transported by these inlets this should be reflected in a higher than expected proportion of birds that inhabited the environments around these "rivers" and the lake. This is in fact

evident; 'wading' birds are the most common element, comprising 93% (n=124) of the avifauna. The other avifaunal elements are much rarer and this is what would be expected if they were only transported via the inlets on rare "chance" occasions.

This theory implies that the 'wading' birds were not, on the whole, transported as far. This is reflected in the fossil specimens: of the 23% of birds within morphological decay stages 1 and 2 (Chapter 2b4) 90% are 'wading' birds (i.e. 20.7% of the total number of specimens (n=124) are wading birds in stages 1 and 2).

By plotting morphological decay stages against the percentage of fossil birds in each decay stage (Figure 6.9) a skewed distribution becomes apparent. The skew is centred over morphological decay stage 2 (complete, articulated bird with no soft tissues/feathers). This implies that the factors that enhance decay/disarticulation (Chapter 2b4) have been inhibited. But as stated above, one of these factors (transport) must have occurred to allow the birds to be fossilised within Lake Messel. Therefore transport of the bird carcasses can not have been prolonged and the individuals must have inhabited the environment around the lake or inlet rivers. As stated above this has been shown to be highly probable as the avifauna contains 93% of this type of bird (the 'wading' birds).

The graph also shows a smaller peak corresponding to morphological decay stage 3.c (disarticulation of the pectoral girdle from the skeleton). This is explained by decay/disarticulation enhancement factors. Lake Messel contained scavengers such as crocodilians and fishes (Schaal and Ziegler, 1992) which may have interacted with some of the carcasses (see Chapter 2b2). Transport may also accelerate disarticulation at certain points: head from neck (morphological decay stage 3.a), legs from pelvis (morphological decay stage 3.b), and pectoral girdle from skeleton (morphological decay stage 3.c) (Chapter 2b4). The disarticulation most likely to be accelerated by transport is the separation of the pectoral girdle from the skeleton. Transport tends to remove anything that "protrudes" from the body (just as it creates a rounded sedimentary particle by removing any rough edges). The pectoral girdle is "torn off" the body with transport over even a short distance as forces act on the large surface area of the wings.

It seems likely that much of the avifauna of Grube Messel was transported into the lake. It represents an assemblage biased towards the 'wading' birds that inhabited the environments nearest to the inlets of Lake Messel.

Preservation

Once the bird cadavers had reached the lake bottom they were protected from scavengers as this environment was anoxic (Schaal and Ziegler 1992, see also Figure 5.4). Anoxic conditions also prevented any further aerobic decay. Rates of burial were variable. Schaal (1992) suggested that sedimentation was episodic and that "turbiditic" currents deposited large amounts of sediment after localised heavy rainfall increased the sediment input to Lake Messel via the two inlets (Figure 6.8). This is consistent with the evidence from fossil birds. The inlet/rivers transporting the birds could also have carried excessive sediment. Schaal (1992) calculated that the normal sedimentation rate was only 10cm per 1000 years, indicating that episodic sedimentation is necessary to explain the preservation of the fossils. Some disarticulated skeletons (especially those that had reached morphological decay stage 3.c) have associated soft tissues/feathers. This also implies rapid burial (Chapter 5) following transport-induced disarticulation shortly after death.

The diagenesis of the bird bones in Grube Messel is unusual. The bones of the avian skeletons all show compaction and crushing (this is the major reason for the large amounts of undescribed material, as it is very difficult to reconstruct bone morphologies for taxonomic analysis). There is little evidence of diagenetic alteration to the skeletal material (the bones are still phosphate) even though the soft tissues are preserved as siderite (Chapter 5). In about 3% (n=128) of the fossil specimens the bones are no longer visible as distinct elements (Figure 6.10) (examples that Peters (1992) described as "mushy" skeletons). In these skeletons the bones have been crushed and then phosphate was precipitated onto the surface presumably by diagenetic pore waters (rich in phosphates) to create the appearance of a "mushy" skeleton. This mineralisation process also resulted in the phosphate layers and “Messelit”, i.e. approximately 1cm diameter ovoid phosphate concretions, that occur throughout the oil shale deposits (pers. obs.; Schaal, 1992).

Summary

Grube Messel has yielded over 128 specimens of fossil birds. These specimens reflect a wide diversity of families but taphonomic effects create a preservational bias towards wading birds (93% of specimens). The specimens are usually articulated (especially the wading birds), but diagenetic effects conceal anatomical details required for taxonomic investigations.

6c. Lacustrine Environment: Green River Formation

6c1. Introduction

The Green River Formation outcrops across three states, Colorado, Utah and Wyoming in the western U.S.A. The first fossil was discovered by Dr. J. Evans and was described as a fossil herring (Leidy 1856). Since then, the Green River Formation has been commercially worked for its well preserved fossils (Grande, 1984).

6c2. Study Methods

All of the birds so far collected from Green River (42 specimens) were reviewed for this study. This review took the form of photographing and making taphonomic observations upon every example (all the specimens were examined in the Smithsonian Institution where Dr. S. Olson had obtained them from other museums to complete a thorough taxonomic revision of the avifauna). This review involved recording the amount and type of disarticulation (later summarised into the decay stages described in chapter 2), presence/type of soft tissues, compaction, diagenesis etc. The data for each specimen was recorded on a *pro forma* (Appendix 6) and then summarised (Appendix 8). All the fossil birds that I surveyed were collected from the commercial quarries in the Fossil Lake deposits.

6c3. Sedimentology and Palaeo-environment

The Green River Formation comprises lacustrine sediments from three Eocene lakes. These lakes were created as foreland basins during the orogeny that uplifted the Rocky Mountains, and then filled with freshwater from the drainage of the nearby tectonic highlands. These freshwater lakes contained a varied and abundant fauna (Grande, 1984).

Faunal and floral comparison of the Green River fossils with similar extant forms indicate that the climate was warm temperate to subtropical. It is assumed to have been similar to the present climate of south eastern U.S.A. (Grande, 1984 and references therein).

The Green River Formation was deposited in three separate lakes: Lake Uinta, Lake Gosiute and Fossil Lake (Figure 6.11). The time ranges for the three lakes are different: Lake Uinta, Late Palaeocene (58 m.y.) to Late Eocene (38 m.y.); Lake Gosiute, Early Eocene (53 m.y.) to Middle Eocene; and Fossil Lake, Early Eocene (52 to 49 m.y.).

The Fossil Lake deposits are the most important source of fossil birds from the Green River Formation (Lake Uinta deposits contain the catastrophic mass mortality horizon of *Presbyornis* (Chapter 4) but these are the only bird

remains that have been recovered from either of the other two lakes). Hence only the deposits of Fossil Lake are considered here.

The Green River Formation of Fossil Lake is divided into the Fossil Butte Member and the Angelo Member (Oriel and Tracey, 1970). The Fossil Butte Member has yielded the avifauna that is reviewed here. This Member is divided into two units, F1 and F2 (Grande, 1984). The F1 unit is a mid lake deposit and the F2 unit is a near-shore deposit (Grande, 1984). Unfortunately, a separate analysis of avian remains in each of the two units is not possible because the specimens collected have little locality data and hence it is impossible to determine from which unit they were recovered.

6c4. Palaeo-ornithology and Faunal Biasing

The palaeo-geographical position of Fossil Lake was similar to the current position of the S.E. U.S.A (e.g. Louisiana). The modern avifauna of such a setting includes a maximum fauna of 24 families (excluding passerines) (Welty and Baptista, 1988). The Eocene avifauna of Fossil Lake (Table 6.3) includes, in contrast, only 5 families.

The avifauna of Fossil Lake contains no true water birds (see Olson, 1985 for definition of a 'water bird'). The lake may have been too deep for them to inhabit (modern waterbirds prefer shallow water). This theory is supported by the presence of *Limnofregata* (the first Frigate bird) - modern Frigate birds inhabit open deep waters, especially open oceans. The other species of birds represented in Fossil Lake probably inhabited the margins of the lake. The actual difference in the number of families between a similar modern environment (24 families) and Fossil Lake (5 families), however, may be largely due to the fact that many families remain undescribed or unrecognised (S. Olson pers. comm. 1992), or had not yet evolved. Thus the apparent under-representation of the fossil avifauna may be an artefact.

6c5. Discussion

Cause of Death

No evidence for the cause of death can be inferred from the fossil bird specimens of the Green River Formation. The most likely causes of death were those proposed by Shipman (1981), i.e. predation, disease, senility, accident and starvation/dehydration.

Biostratinomy

From the faunal list (Table 6.3) it is evident that no true waterbirds are present. Thus the fauna must have been transported into the lake (as deaths on the wing whilst over the lake would have been exceptionally rare). The

effects of transport could be to increase the rate of decay/disarticulation (Chapter 2b7). This is apparent in Figure 6.12 which shows the percentage of birds in each morphological decay stage. The majority of birds are disarticulated; 76% of specimens (n = 42) can be placed into stages 3a to 5 (Chapter 2b4). Although factors other than transport influence disarticulation, their effects are neglible. Grande (1984, p. 182-185) showed that the rate of burial was high and that scavenging of the carcasses by aquatic organisms was prevented by anoxic stratification. Therefore transport was the major cause of decay/disarticulation. This is reflected in the rate of disarticulation of the pectoral girdle from the body which results in a peak on the graph (Figure 6.12) at stage 3.c. 24% (i.e 10 specimens, n=42) of the fossil bird specimens are well preserved (stages 1 and 2), which implies that they were not transported very far before entering the lake. Of these 10 well preserved specimens, 8 are wading birds. These birds were clearly not transported far as the wading birds inhabited the lake margins (it is also implied that the other 2 well preserved birds were not transported far, and therefore they must have died within the immediate vicinity of the lake).

Preservation

The preservation of avian soft tissue in the Green River Formation of Fossil Lake is limited to feathers. The feathers are preserved as "carbonised traces" (type B preservation, Chapter 5). The bones remain as the original phosphate (hydroxy-apatite) (XRD analysis by Dr. P.R. Wilby). The only post-burial effects that the bones show are compaction. All the bones are crushed to a great extent. Figure 2.37 shows a skull of *Pseudocrypturus cercanaxius* that would have been approximately 3 cm wide across the post-otic cranium, whereas the fossil skull is now only 1mm wide at the same point.

Summary

The Green River Formation has yielded 42 specimens of fossil birds. The specimens reflect a rounded avifauna (i.e. no taphonomic bias) and the low diversity of families (n=5) is due to a lack of taxonomic description. The specimens are generally partially disarticulated, but the skeletons are diagenetically well preserved.

6d. Lagoonal Environment: Solnhofen Lithographic Limestone

6d1. Introduction

The fauna of the Solnhofen Limestone is one of the most famous among Konservat Lagerstätten due to the occurrence of *Archaeopteryx lithographica,* the so called Darwinian "missing link" between dinosaurs and birds. Apart from *Archaeopteryx* this Lagerstatte contains other flying vertebrates such as rhamphorhynchoid and pterodactyloid pterosaurs, and the small, non-flying, coelurosaurian dinosaur *Compsognathus longipes*, which may for all intents and purposes be treated as a small featherless bird (although some authors - e.g. Paul (1988) and Bakker (1986) - contend that some dinosaurs, especially the avetheropods (like *Compsognathus*) were feathered). As will be shown later, the carcass of *Compsognathus* behaved taphonomically in a similar way to *Archaeopteryx.*

Most of the literature on *Archaeopteryx* is concerned with the taxonomy, evolution and palaeobiology of the seven known skeletal specimens e.g. Ostrom (1972, 1973, 1974, 1975a+b, 1976); Walker (1972, 1980, 1985); Wellnhofer (1974, 1985, 1988a, 1993). The taphonomy of *Archaeopteryx* has also been investigated (Heller, 1959; Rau, 1969; Barthel, 1970 and 1978; Rietschel, 1976; Helms, 1982; Wellnhofer, 1983; de Buisonjé, 1985; Viohl, 1985; Swinburne, 1988; Barthel *et al.*, 1990), and the recent controversy upon the authenticity of the specimens inadvertently added further taphonomic data to the literature (Hoyle *et al.*, 1985; Watkins *et al.*, 1985a, b and c; Howgate, 1985; Charig *et al.*, 1986; Hoyle and Wickramasinge, 1986; Swinburne, 1988).

6d2. Study Methods

All the skeletal specimens of *Archaeopteryx* and *Compsognathus* were reviewed for this study. This review took the form of making taphonomic observations upon every specimen from the literature except in the case of the London specimen of *Archaeopteryx* where direct observations were conducted. Records were made of the amount and type of disarticulation (later summarised into the decay stages described in chapter 2), presence/type of soft tissues, compaction, diagenesis etc. The data for each specimen was recorded on a *pro forma* (Appendix 6) and then summarised (this data does not appear in Appendix 8 because it is widely available from the literature). Previous work upon the taphonomic aspects of *Archaeopteryx*, *Compsognathus* and the pterosaurs is reviewed in the following sections.

6d3. Sedimentological Evidence

Seilacher *et al.* (1985) remarked that diagenesis is traditionally viewed as the result of physiochemical processes, but in Solnhofen the preservation of soft tissues and the solution of aragonite seem to have been controlled by microbiological activity. Seilacher *et al.* (1985) illustrated preserved trackways and roll marks (Plate 1, Figures 4-9, facing page 14) which demonstrate that a macroscopic scum occurred on the sediment surface. They argued that the effects of such a scum are:-

1. To protect soft sediments against erosion.
2. To favour the preservation of tracks and other markings.
3. To serve as a food source during benthic events.
4. To protect carcasses against decay.
5. To act as a carbonate pump into the sediment.
6. To seal the particular microenvironments responsible for the absence of bioturbation and for the unusual preservational histories of ordinary fossils such as ammonite shells.

The most important factors in the preservation of *Archaeopteryx* are 1, 2, and 4.

Barthel *et al.* (1990) stated that *Archaeopteryx* lived in a terrestrial environment to the north of the lagoon. Because there is no trace of this terrestrial environment this palaeoecological reconstruction must be somewhat speculative, but up to the present time the theory presented by Barthel *et al.* (1990) is the most complete that is available. The following is their description of this landmass.

> ..... In all probability the land was low-lying and of no great areal extent because it did not supply any appreciable amount of terrigenous sediment to the lagoon. River channels were not a permanent feature of the landscape, but freshwater ponds probably existed seasonally. There may have been a belt of wide sandy beaches fringing the land.
>
> In the hinterland, the stunted, shrubby growth consisted mostly of gymnosperms, able to survive in this dry, salty soil. Seed ferns, particularly the widely dispersed and presumably hardy *Cycadopteris*, formed a scanty undergrowth whilst squat, cone-bearing cycadophytes, deciduous-leaved ginkgos and stunted, scaly conifer bushes were present as isolated shrubs. No logs have ever been recovered from the Solnhofen Plattenkalk and one conclusion may be that trees were either very rare or absent from the land immediately adjacent to the lagoon. However, further to the north lay the landmasses of the 'Mitteldeutsche Schwelle' and the London-Brabant Massif and they most probably held richer plant as well as animal communities. The plants produced various megaspores, cones and pollen, which would have supported a diverse insect population. Of the insects recovered from the

Solnhofen Plattenkalk, most are dependent on a freshwater habitat for the larval stages of their life cycle.

Into this setting we can place the land reptiles and the renowned *Archaeopteryx*. The rhynchocephalians and small lizards most likely spent much of their lives basking in the sun and running under stones. They probably ate insects and were themselves eaten by the fast-running little dinosaur *Compsognathus* (a lizard has been found in the gut contents of the one known specimen of *Compsognathus*). The relatively common pterosaurs lived in close proximity to the lagoon and with their large wings and light bodies they must have been adept fliers. Some were probably water animals as they have webbing between their hind toes and many ate fish, judging from the stomach contents. However, one [pterosaur] genus, *Ctenochasma*, has teeth, which suggest that it was more likely to have been an insectivore. Barthel *et al.*, 1990, p. 86.

Barthel *et al.* (1990) speculated that *Archaeopteryx* would have lived an arboreal existence (to avoid predators and because *Archaeopteryx* could not have run fast enough for take off). No trees are found fossilized in the lagoon, implying that *Archaeopteryx* could have been buried at quite some distance from its normal habitat.

Barthel *et al.* (1990) also considered the biostratinomy of *Archaeopteryx* and concluded that airborne individuals were caught in high winds and waves and were drowned. With the lungs full of water and the plumage soaked, the bodies sank to the bottom. They noted that modern bird carcasses show the same initial stages of decay as in *Archaeopteryx* i.e. in *Archaeopteryx* feathers are only preserved on the wings and the tail (and possibly the back of the head) and in modern birds the loosely attached contour and down feathers are lost from the back and the breast and the most strongly attached flight feathers remain for the longest time.

6d4. Evidence for the transport of *Archaeopteryx* and causes of disarticulation

De Beer (1954) stated that some earlier authors, particularly R. Owen and H. Steiner, believed, erroneously, that the London specimen was prey to other animals before entombment and that this explained the disarticulation pattern. He suggested that the specimen was more likely to have fallen onto a mud-flat near the shore of the Solnhofen sea where it underwent gentle disarticulation before becoming covered with sediment. De Beer (1954, p.7) went on to remark that the way up of the slabs was not recorded when collected but, because the feather impressions on the main slab were more distinct, then this must be the underslab, for the following reason:

> ..... It must be supposed that when the body of the bird fell on to the surface of the mud, the impressions made by the impact of the feathers on that surface were protected from disturbance and water movement by the overlying feathers themselves. The subsequent deposition of the fine grained matter on the upturned surface of the feathers would, however, not be so protected from the limited movement of the water which, it is clear, must have taken place and been responsible for the displacement of the head a few inches from its original resting place.

Barthel (1970) stated *Archaeopteryx* specimens had been found in "awkward mummy-like conditions" which are consistent with birds that dry and mummify on a shoreline. These shoreline mummies can be buried at sea if a very high tide coupled with a seaward wind drifts the mummies offshore where they eventually sink.

Barthel noted that the distance from the palaeo-shoreline could be directly correlated with the degree of preservation in *Archaeopteryx,* i.e. those in a near shore environment (Berlin *Archaeopteryx*) are well preserved and the further away from the shoreline the more decay the specimens have undergone.

Barthel also noted that *Archaeopteryx* would be less subject to prolonged drift because the bones are less pneumatic than modern birds. It also has a large heavy tail, therefore only the feathers and the mummified parts remaining would have retarded sinking.

Viohl (1985) stated that *Archaeopteryx* was undoubtedly capable of powered flight (a view supported by Norberg, 1985) and this flight ability is indicated by the complete preservation of the Berlin and Eichstätt specimens. His theory precludes long transport and rapid burial. He assumed that the birds flew across the sea, perhaps from one island to another, when they were caught in a storm or monsoonal shower and drowned. The lungs then filled with water, and the plumage was soaked. Only in this condition would the carcasses sink down quickly, as was stated by Rietschel (1976). Otherwise they would have floated for a prolonged time, becoming more disarticulated (noted by Schäfer 1955, 1962, 1976).

6d5. Pose of the *Archaeopteryx* skeletons

Heinroth (1923) used magpies and Australian pheasant cucals in experiments to investigate the 'bicycling pose' of the Berlin *Archaeopteryx.* He arranged the cadavers in the position of *Archaeopteryx.* He used fresh unplucked, plucked and defleshed specimens. He ascertained that after artificial detachment of the muscles and also some slight decay the carcass adopted a position similar to *Archaeopteryx.* He noted that, after muscle

tension has disappeared, the pull of the ligaments creates the neck curvature as seen in *Archaeopteryx*. Also in *rigor mortis*, the antagonistic muscles all contract at the same time giving the same appearance as in *Archaeopteryx* specimens.

Moodie (1923) noted that *Archaeopteryx*, *Compsognathus* and some pterosaurs exhibit a pronounced opisthotonos, "a tetanic spasm in which the spine and extremities are bent with convexity forward, the body resting on the head and heels" (Moodie 1923, p.323). He attributed such a spastic spasm to the poisoning of the central nervous system by bacterial poisons, mineral poisons or other toxins, which when liberated in the blood, attack the brain and spinal cord. This, however, is not believed to be correct. It is more likely to be due to desiccation as Heinroth (1923) assumed.

Weigelt (1929/1989, p.105-106) argued that the curvature of the neck (the backward bend placing the head above the centre of the back) in the land/flying vertebrates from Solnhofen is a result of desiccation and shortening of muscles and tendons after *rigor mortis* has finished.

Rietschel (1976) indicated that wind-driven near-surface currents operated from east to west which led to the transport of *Archaeopteryx* on the water surface in an east to west direction. He also suggested that *Archaeopteryx* died by eating poisoned fish or invertebrates that were washed up on the lagoon shoreline. The dead *Archaeopteryx* then would have floated for several days before sinking with the head and neck dorsally bent. He postulated that the head and neck would have come to rest in this position on the sediment surface thus explaining this configuration in the fossil specimens.

I repeated Heinroth's basic experiment using a pigeon (*Columba livra*). The pigeon was defleshed by removing all soft tisssues by dissection. The pigeon was then placed in a fume cupboard with the extraction unit switched on. This allowed a constant stream of air of room temperature (20°C) to pass over the specimen. The specimen was left for three days. As in Heinroth's (1923) experiment the neck curved backwards and the legs assumed the 'bicycling pose' evident in *Archaeopteryx*. The carcass adopts this pose because, without the muscles to act as an antagonistic force to the dessicating and shortening tendons, the skeleton contorts into the 'bicycling pose'. It is reasonable to assume that this same pose would occur if the muscle tissue of *Archaeopteryx* had first decayed away naturally before dessication.

6d6. Preservation of the Feathers of *Archaeopteryx*

Rietschel (1985) summarised previous interpretations of the preservation of the feathers of *Archaeopteryx* as "impressions" of the feathers

on the soft sediment surface. He argued that this was impossible (based on current understanding of how the Solnhofen limestone was deposited) and that preservation could only have resulted from:- 1) the plumage being covered with a very fine grained sediment or, 2) conserved by an overgrowth of bacteria and algae. He termed these mechanisms "precipitation". A thorough review of the preservation of the feathers of *Archaeopteryx* is presented in Chapter 5.

6d7. Preservation of Pterosaurs and *Compsognathus*

The pterosaurs provide comparative data as the only other group of flying vertebrates represented in the Solnhofen Limestone. *Compsognathus* is very similar both morphologically and taphonomically to *Archaeopteryx*, even though *Compsognathus* did not fly.

De Buisonjé (1985) suggested that the backward twist of the neck in pterosaurs is due to their being killed by ingesting toxin-filled coccolithophorans or fish poisoned by such a bloom (modern coccolithophoran blooms may poison fish: Brongersma-Saunders, 1957) and then drifting for some days before sinking to the bottom. Some buoyancy in the chest region kept the carcasses afloat with the head and neck hanging dorsally bent, essentially in the same position in which they finally came to rest on the bottom.

Wellnhofer (1970) looked at the preservation of the pterodactyloid pterosaurs, and made similar observations to those of Barthel (1970) on *Archaeopteryx*. He noted mummification of Solnhofen pterosaurs on the lagoon shoreline before entombment, and also observed that the further from the palaeo-shoreline the animal was buried (i.e. the longer the carcass had drifted) the more disarticulated it became.

Ostrom (1978) studied the osteology of *Compsognathus longipes* Wagner and noted that the bones are preserved as actual bony elements or as impressions; the bony elements are completely replaced by calcite with no re-crystallisation and consequent distortion or loss of detail. The specimen was close to the ground surface in the quarries and consequently subject to solution by sub-surface run-off. This weathering caused unusual textures which have been interpreted as skin and muscle preservation by other authors (von Huene, 1901; Nopsca, 1903).

Ostrom further noted that the specimen is preserved on its right hand side and the hands, skull, cervical ribs and posterior gastralia show some disarticulation. According to Ostrom this disarticulation pattern is due to scavengers or more likely the action of gentle bottom currents which dispersed the bones after their connecting tissue decayed. The fact that

stomach contents are present indicates that the peroneal cavity was not breached before burial. The disarticulation of the posterior gastralia may be due to eruption of decomposition gases from this region when the carcass was on the lagoon floor.

Wellnhofer (1988b) noted that if Solnhofen pterosaurs were bipedal, their mode of preservation would be as in *Archaeopteryx* and *Compsognathus* (i.e. spread wings embedded dorso-ventrally and hind legs still in acetabular articulation, although directed to one side). He used this to support the case for pterosaur quadrupedal locomotion.

6d8. Discussion

Cause of Death

The cause of death of *Archaeopteryx* can never be ascertained although it was not due to predation (as revealed by the fully articulated nature of the specimens and the fact that no bones of *Archaeopteryx* show signs of biting or gnawing (pers. obs.)). Moodie (1923) argued that the 'bicycling pose' was due to poisoning of the nervous system. It is more likely that this is incorrect and the posture of *Archaeopteryx* and *Compsognathus* is due to osmotic dessication of the tendons. The curved posture is also evident in fish and crustaceans (Barthel *et al.*, 1990).

Biostratinomy

If *Archaeopteryx* and *Compsognathus* were terrestrial animals and they lived on the supposed land mass to the north of the lagoon (Barthel *et al.*, 1990) then we must explain their presence within the Solnhofen sediments. We must also explain their rarity in relation to the pterosaurs. The pterosaurs have two principal feeding habitats (Table 6.4) and these indicate two differing ecologies. The piscivorous forms must have fed over the sea (there is no evidence that any fish lived in the lagoon (Barthel *et al.*, 1990)) and the insectivorous forms would have fed near to the land mass (insects rarely live over salt-water and the insects preserved at Solnhofen all require freshwater for their larval stages). As can be deduced from Table 6.4 the piscivorous forms probably flew regularly over the lagoon to their marine feeding habitats, thus giving them a higher preservation potential in the lagoon sediments. But if the insectivorous forms were mainly terrestrial why are they more numerous (Table 6.4) than *Archaeopteryx*? I suggest five possible explanations:

1) Terrestrial pterosaurs were more common than *Archaeopteryx*, i.e. the apparent relative abundances (Table 6.4) are an actual representation of the real abundances in the terrestrial ecosystem.

2) The flying ability of *Archaeopteryx* was poor and it behaved ecologically like a small coelurosaurian dinosaur. This can probably be discounted as there is convincing evidence that *Archaeopteryx* was a capable flier (Rietschel, 1985; Norberg, 1985).
3) Insectivorous pterosaurs were more likely to frequent the lagoonal area and hence have a higher preservation potential.
4) Insectivorous pterosaurs spent more time on the wing and therefore had a higher chance of being blown over the lagoon and drowned by storms and strong winds (the palaeo-latitude of the lagoon was within the monsoonal region).
5) Pterosaurs had a waterproof pelage which allowed them to settle on water hence increasing their preservation potential.

Of all of these hypothetical solutions I regard the first as the most probable. It is most likely that *Archaeopteryx* and *Compsognathus* were the top predators on the land mass (as there is no evidence of the presence of larger predators, apart from crocodilians). As ecological studies have shown that the numbers of individuals at the top of an ecosystem or food web is small, the apparent rarity of *Archaeopteryx* and *Compsognathus* can easily be explained.

The biostratinomy of *Archaeopteryx* has been explained by high winds and storms blowing individuals over the lagoon where they were drowned. This cannot be true for *Compsognathus*. The specimen of *Compsognathus* is well articulated and there is no evidence that the soft tissues decayed before the specimen reached the lagoon floor (pers. obs.). As palaeo-temperatures for the surface waters of the lagoon were in the region of 26°C (Engst, 1961), temperatures on land must have been higher. These temperatures are similar to those used in my actualistic experiments (Chapter 2b6). The rate of decay was shown to be very rapid (skeletonisation within 1 to 3 days). Therefore the period of time from the point of death to entombment in the sediments is unlikely to have been very long (1 to 2 days). This now begs the question of how *Compsognathus* became entrained in the lagoon so quickly. I believe that if the climate were semi-arid with a low annual rainfall (Barthel *et al.*, 1990) then a storm or heavy rain would have created flooding. This water would be subject to rapid surface runoff. It is possible that *Compsognathus* was caught by this fast moving water and swept into the lagoon and buried quickly by the turbid water and sediment. The more exquisitely preserved *Archaeopteryx* specimens (the Berlin, Eichstätt and Solnhofen) may well have been preserved in this way although the hypothesis that they were caught in high winds and drowned could still be valid.

All the terrestrial animals have been found in the Kelheim and Eichstätt regions (Barthel *et al.*, 1990) (Figure 6.13), which is also the source of the best preserved *Archaeopteryx* specimens. Therefore I have assumed that these well preserved *Archaeopteryx* specimens had a similar taphonomic history to *Compsognathus*, because to be well preserved *Archaeopteryx* could not have been transported far from its place of death. The other three *Archaeopteryx* specimens show a greater degree of disarticulation (corresponding to stage 3.f on the disarticulation scale proposed in Chapter 2) and this is to be expected if the specimens were transported for a greater distance (Figure 6.14). This point raises the further question of why some specimens were transported further than others. I believe that the following factors explain this anomaly:

1) *Archaeopteryx* was carried out over the lagoon, whilst still alive, and then drowned.
2) The currents created by the surface runoff were stronger, due to very high levels of rainfall.
3) Not all birds float (contra Schäfer, 1972; see Chapter 2) and this may have been true for *Archaeopteryx*, whose bones were much denser and less pneumatised than modern birds. In order to allow *Archaeopteryx* to float for long periods of time, the carcass must have started to decay. This was necessary to bloat the carcass with decay gases and render it buoyant). This processes could only have persisted for several days or the specimen would have disarticulated to a greater extent.
4) It is accepted that Solnhofen was hypersaline, which of course would have increased its buoyancy properties (e.g. the Dead Sea) but Barthel *et al.* (1990) noted that the climatological factors that created the preservation opportunity would also destroy this hypersalinity by mixing of the water. Therefore hypersalinity cannot explain the floating of the carcasses for prolonged periods.

Further evidence for the above factors can be deduced from Figure 6.15. This graph of percentage of specimens in category versus morphological decay stage shows two peaks corresponding to stage 2 and stage 3.e. If there were only two basins in which the preservation could have occurred, and transport occurred from one basin to the other, then the *Archaeopteryx* skeletons deposited in the nearest basin to the shore (the Eichstätt basin) would be better preserved than those in the further basin (the Solnhofen basin). Because the specimens are disarticulating whilst being transported only certain morphological decay stages would be preserved. The two peaks in Figure 6.15 correspond to deposition in each of the two

basins. This further emphasizes that transport was from east to west and that exceptional preservation was limited to these basins of deposition.

Preservation

Once the well preserved *Archaeopteryx* and *Compsognathus* had reached the lagoon floor they would have been covered quickly with sediment that had been resuspended by the turbulent action of the currents transporting the carcass. The carcass would have decayed undisturbed under the sediment so preventing further disarticulation. The preservation of the feathers requires special conditions (Chapter 5). The other specimens of *Archaeopteryx* (the London, Maxberg and Taylor) specimens eventually came to rest on the lagoon floor, but not in turbid conditions thus allowing them to disarticulate further before being covered with sediment. There is evidence of periodic current activity on the lagoon floor (Barthel *et al.* 1990) and this would further disarticulate and scatter the skeletal elements (Chapter 2).

Seilacher (1985) and Gall (1990) demonstrated that microbial films (bacterial jelly) are very important in the preservation of soft bodied fossils in lithographic limestones, and it is likely that they affect the preservation of all fossils in lithographic limestones. There is a smooth area of sediment around the skeleton of *Archaeopteryx* which differs markedly in texture to the surrounding matrix (the London specimen, pers. obs.). This was used to argue that *Archaeopteryx* is a forgery (Hoyle and Wickramasinge, 1986). Charig *et al.* (1986), however explained the smooth area as "the impression of the animal's cadaver upon parts of the surface. (A similar difference in texture may be seen between a human footprint on a mud-flat and the general surface of the surrounding mud)."

In the light of Seilacher *et al.* (1985) and Gall (1990) this duality of texture is more likely to be the effect of a microbial veil / sediment interaction. The sedimentary layers around *Archaeopteryx* have not been compacted to the same degree as the surrounding limestone. This too can be explained by the microbial veil theory. If the cadaver had a veil covering it and extending into the surrounding sediment, it would promote early diagenesis (e.g. Pye *et al.* 1990 described early diagenesis of siderite due to microbial activity). If diagenesis in these regions is early then the differential compaction observed will occur. The diagenesis of the *Archaeopteryx* fossils is quite straightforward in comparison to their biostratinomy. Once the carcass had been covered with sediment this effectively sealed it from the porewaters. It would rapidly form a micro-environment in which reducing conditions predominated (due to decomposition of the organic matter). These conditions would retard decay and increase soft tissue preservation, e.g. the feathers (Chapter 5).

The actual skeletal elements have undergone little diagenetic change. The bone is still preserved as calcium phosphate (hydroxyapatite), the organic constituents (e.g. collagen) having decayed away. The cavities within the bone have formed sites of diagenetic calcite growth and this is evident where the fragile fossil bone is flaked away on the London specimen (pers. obs.).

Summary

The Solnhofen Lithographic Limestone has yielded 7 specimens of *Archaeopteryx* (two species). As far as can be assessed this represents the complete diversity of birds. *Archaeopteryx* lived on the landmass to the north and transport (with decay) to its place of deposition accounts for the nature of preservation. The specimens are diagenetically well preserved which has allowed much data of taxonomic significance to be obtained from the skeleton.

6e. Marine Environment: La Meseta Formation

6e1. Introduction

Seymour Island is situated about 100km S.E. of the Antarctic Peninsula. It has an area of about 150km^2. The first fossils from the Eocene, La Meseta Formation were collected by C.A. Larsen in 1893 whilst acting as a scientific officer on a Norwegian whaling ship.

6e2. Study Methods

All of the birds so far collected from the La Meseta Formation were reviewed for this study. This review took the form of making taphonomic observations upon every specimen. This involved recording the amount and type of disarticulation (later summarised into the decay stages described in chapter 2), bone brakeage, compaction, diagenesis etc. The data for each specimen was recorded on a *pro forma* (Appendix 6) and then summarised (this data does not appear in Appendix 8 because it only consists of a list of museum numbers and bone identification). The vertebrate fauna of the La Meseta Formation comprises birds, fish (sharks) and mammals (seals, whales and marsupials) (Elliot *et al.*, 1975; Case *et al.*, 1988). The avian material was described by Wiman (1905), Marples (1953) and Simpson (1971), who focused on the material of Spheniscidae (penguins). Case *et al.* (1987) described a solitary phalanx referable to the Phororhacidae. I compiled a faunal list (Table 6.5) based on specimens in the Smithsonian Institution (Washington D.C.), which contains the complete collections of the American expeditions to Seymour Island during the 1970's.

6e3. Sedimentology and Palaeo-environment

The island consists of Cretaceous sediments in the south and mainly Tertiary strata in the north (Figure 6.16). This summary will concentrate on these Tertiary sediments and, in particular, the Eocene La Meseta Formation in which the avian remains have been found.

The bird fossils were recovered from two horizons within the La Meseta Formation (W. J. Zinsmeister pers. comm.). These horizons are unconsolidated and consist of laminated, fine grained, grey sand alternating with dark, silty clay layers, light grey well sorted fine sands and mottled brownish grey to greenish/grey bioturbated silty sand (Telms III and V of Elliot *et al.*, 1975).

These horizons displays sedimentary structures which include ripple-drift cross lamination sets, planar cross bedding, oscillation ripple marks and both small and large scale cut and fill channels (Elliot *et al.*, 1975). Elliot *et al.* (1975) inferred from these structures that the direction of sediment transport

was south-easterly and away from a northeast-southwest trending shoreline. They also concluded that these sediments were probably deposited in a high energy, nearshore deltaic and shallow marine environment.

Further evidence for this hypothesis was reported by Wiedman *et al.* (1988) who used brachiopods to deduce that the deposits were late Eocene in age and that the palaeo-environment was shallow nearshore marine, and dominated by wave and tide action. This was corroborated by Zullo *et al.* (1988) using fossil barnacles. They argued that the preservation of complete specimens of barnacles still attached to pebbles indicated that rapid burial occurred similar to that in high-stand deposits of coastal onlap sequences.

Evidence for the palaeo-environment of the land mass was derived from palynological studies (Askin, 1988; Case, 1988). The vegetation was podocarp dominated which suggests a cool temperate climate with prevalent moist conditions, e.g. similar to the present day lowland of southern Chile.

6e4. Palaeo-ornithology and Faunal Biasing

Of the 1242 specimens (all isolated bones) 99.3% are Spheniscidae remains. The Spheniscidae of the La Meseta Formation have been classified into 8 genera and 12 species (Simpson, 1971) (Table 6.6).

From these data it is evident that the avifauna is highly biased. The present day fauna of the Antarctic South Pacific is shown in Table 6.7. Censuses of modern Antarctic species are not complete but recent estimates (Fothergill, 1993) indicated that there are 34-40 million Spheniscidae, 250000 Diomedeidae and 150 million Procellariidae. Thus in the modern Antarctic environment less than 33% (based on numbers of individuals) of the avifauna is comprised of the family Spheniscidae whereas the Eocene Seymour Island assemblage contained 99.3% (pres. obs. and Fothergill, 1993).

The absence of expected families is due to the fact that all the families (apart from the Spheniscidae and Anatidae) that comprise the modern avifauna had not yet evolved. This allowed the Spheniscidae to radiate and adapt to a range of ecological niches (as shown by the fact that 15 species - Table 6.6 - existed during the Eocene whereas only 7 species are present in the modern avifauna) and completely dominate the avifauna. There is also faunal biasing caused by ecological factors. The coastal environment was not inhabited by terrestrial or freshwater aquatic birds (e.g. bustards, cranes, and Phororhacidae) which are therefore underrepresented (Table 6.6).

6e5. Discussion

Cause of Death

The cause of death can never be totally ascertained but it is possible to postulate likely causes. Antarctic environments are harsh, therefore mortalities will be high. The vertebrate fauna of the La Meseta Formation contains sharks, seals and whales all which would have preyed on the avifauna (Figure 6.17). Ninety percent of the fossil avian bones are broken (Figure 6.18) which may be due to predation though it is more likely, however, to have been due to transport effects (see below).

Biostratinomy

Modern penguins inhabit coastal environments, and it is reasonable to assume that the Eocene forms of the La Meseta Formation also inhabited this environment (this is supported by the fact that the La Meseta Formation is interpreted as representing a coastal setting: Chapter 6e2 above). This coastal environment was high energy and wave and tide dominated resulting in rapid disarticulation and fragmentation of avian skeletons (Figure 6.18). Figure 6.18 shows that 90% of the avian bones recovered were broken indicating that high energy transport was involved (Napawongse, 1981). Predation/scavenging was a minor factor; close examination of the bones reveals "severe" abrasion indicative of high energy transport (e.g. the trochlae of tarsometatarsi, and the deltoid crests of humeri have been abraded away). Figure 6.18 also shows that thin walled, "fragile" bones such as the skull, vertebrae, and fibula are always broken whereas the more "robust" bones of the skeleton such as the humeri and tarsometatarsi (Figure 1.3) may be complete. This indicates that transport is the dominant influence (Figure 6.20). If predation/scavenging was responsible, complete bones would appear in all skeletal element categories; a predator will break bones regardless of "robustness" but the effects of transport only affects "robust" bones after prolonged periods.

Decay in Antarctic conditions is slow (Chapter 2b6, Appendix 2), as decay rate is influenced by temperature. The expected time required for skeletonisation is about 39 days (using Equation 2.2, Chapter 2b6, and assuming a value of sea temperature = 6°C which gives a value for $\psi = 0.177$, W/Wo = 0.25 as the average skeleton of a penguin weighs 0.25 of its live mass).

In a harsh environment such as the Antarctic, high amounts of scavenging are inevitable (Figure 6.19) because a carcass provides easily obtained food. In the modern environment an Adelie penguin (*Pygoscelis antarctica*) that was killed by a Leopard Seal (Figure 6.17) was filmed with

time lapse photography as it decayed on the seafloor. The carcass was completely skeletonised within 36 hours by one metre long nemertean worms (Fothergill 1993). Thus the rate of degradation in this environment may be accelerated by scavengers.

A variety of decay/disarticulation inhibiting factors are required to preserve articulated skeletons (Chapter 2b7). These did not prevail in the environment of the La Meseta Formation which was characterised by "normal" marine conditions (albeit with low sea temperatures). In contrast, high energy transport led to the formation of a Konzentrat-Lagerstatte (*sensu* Seilacher *et al.* 1985) of avian bones.

Preservation

The state of preservation of the bones of the fossil avifauna of the La Meseta Formation is not unusual. There has been no diagenesis of the deposits (the sands are unconsolidated) and only slight compaction has occurred. The bones have only been slighly altered: the organics (collagen) have decayed away and minerals have precipitated resulting in a black colouration (pers. obs.). The bones found on the surface of outcrops, however, have been subjected to the modern climatic conditions of Seymour Island. The very low temperatures have caused the bones to exfoliate and crack and have caused unusual mineral growths on the bone surface (turquoise in colour). Fortunately the collectors of the bones retained all fragments so modern weathering effects can be distinguished from those of ancient taphonomic processes.

Summary

The La Meseta Formation has yielded 1242 specimens of fossil bird bones. These specimens represent a low diversity avifauna which is dominated by penguins (99.3% of the avifauna). This low diversity may be a real reflection of avifaunal diversity of the coastal palaeo-environment of the La Meseta Formation. The specimens are all isolated bones which have been biased (due to transport) towards the more robust/heavily ossified skeletal elements.

6f. "Trap Environment": Rancho La Brea

6f1. Introduction

Rancho La brea is a "trap" deposit (*sensu* Seilacher *et al.*, 1985). Rancho La Brea is comprised of asphalt deposits and is located on the outskirts of Los Angeles, California, U.S.A. It has proved to be one of the richest sources of Pleistocene vertebrate remains in the world. It has been estimated that over one million bones have been excavated (Sutcliffe, 1986). Not only the quantity and quality of the vertebrate material but the associated fauna and flora have provided palaeontologists an unrivalled opportunity for palaeo-ecological and taphonomic studies.

6f2. Study Methods

The collections of avian material from Rancho la Brea in the Smithsonian Institution were reviewed for this study. This review took the form of making taphonomic observations upon every specimen. To compliment the studies of specimens the detailed numbers of specimens and taxonomic descriptions published within the scientific literature were also reviewed (e.g. Stock, 1956). This involved recording the amount and type of disarticulation (later summarised into the decay stages described in chapter 2), bone brakeage, compaction, diagenesis etc. The data for each specimen was recorded on a *pro forma* (Appendix 6) and then summarised (this data does not appear in Appendix 8 because it only consists of a list of museum numbers and bone identification).

6f3. Sedimentology and Palaeo-environment

The asphalt deposits of Rancho La Brea originate in the underlying Miocene Puente Group Shales. The oil migrated from these sediments (via structural faults) and was deposited within the Pleistocene, terrestrial, Palos Verdes Sand (Sutcliffe, 1986). Where the oil seeped to the surface its viscosity gradually increased (due to lower temperature, oxidation and the loss of volatiles) and it became asphalt.

Old ideas that pools of liquid asphalt entrapped the animals which were then disarticulated by internal convection currents are now known to be erroneous (Sutcliffe, 1986). Sutcliffe (1986) stated that the fossiliferous strata at Rancho La Brea accumulated principally as a gradual build up of fluviatile sediments on a series of old land surfaces, during a period of time when asphalt seepage was taking place discontinuously. Studies of insect remains showed that some of the carcasses had remained unburied on the surface of the ground for as long as seven months (Sutcliffe, 1986). Stream action by itself, however, although it may have reworked some of the bone deposits,

was insufficient to account for the total accumulation of bone deposits at Rancho La Brea (Sutcliffe, 1986). When obscured by leaves and other debris the asphalt seepages would have been a hazard to birds which might accidentally have become mired by the feet, or by "tarring" of their feathers. After death, trapped animals would usually fall on to one side so that the limbs and the underside became buried in asphalt, whilst the rest of the carcass was exposed. Predatory mammals and birds would remove exposed parts of the carcass (which explains why bones of the lower limbs are more abundantly preserved than others) sometimes becoming trapped themselves.

Some of the bone deposits have apparently been secondarily impregnated with seeping asphalt after deposition. It is evident that the distribution of fossil bones is to some extent controlled by the deposition of the asphalt which acted as a preserving medium; bones in non-asphaltic parts of the deposits are often in a poor state of preservation and may even have disappeared (Sutcliffe, 1986).

Palaeo-botanical studies indicate a cool, humid coastline with at least 50cm of rainfall per annum, with occasional drier grassland situations inland (Sutcliffe, 1986). This palaeo-environment can be compared to present day environments in the states of Washington and Oregon on the western seaboard of the U.S.A.

6f4. Palaeo-ornithology and Faunal biasing

The avifauna of Rancho La Brea (Table 6.8) is very similar to the present day fauna of the western seaboard of the U.S.A. (for example all the taxa comprising the avifauna of Rancho La Brea are present in the modern avifauna of Oregon, pers. obs. and Gabrielson and Jewett, 1940). There are only two major differences between the Pleistocene and the present avifauna:

1. The high proportion of "birds of prey" within Rancho La Brea.
2. The low diversity of passerine (=Passeriformes) families within Rancho La Brea.

The large proportion of the Rancho La Brea avifauna consists of birds of prey (67% of species: Table 6.8). This disproportionate percentage of "carnivores" is also duplicated within the mammal fauna (Sutcliffe, 1986), and can be explained by the fact that "carnivores" were attracted to the asphalt by the abundance of food (trapped carcasses) and became stuck themselves whilst trying to reach these carcasses. This also explains why day-flying birds of prey (Falconiformes), which hunt by sight, are more numerous than the night-flying owls (Strigiformes), which hunt mainly by sound (Table 6.8) (pers. obs.).

The low diversity of passerine birds has two possible explanations.

1. The Passeriformes only appeared at the beginning of the Pliocene and new families only started appearing during the Pleistocene (Unwin, 1993). Thus the low diversity at Rancho La Brea may be real".

2. It is likely that the passerines were feeding on the carrion already entrapped (the passerine assemblage consists of 4 genera, three of which were ravens, magpies and shrikes, all of which primarily feed on carrion). Other passerine families do not feed primarily on carrion, so the low diversity may reflect feeding habits.

The remaining avifauna consists of a "wetland assemblage" suggesting that there were standing bodies of water or water courses in the Rancho La Brea area. This conclusion is supported by the presence of amphibians and turtles (Sutcliffe, 1986). If these water bodies formed upon the asphalt, wetland birds would have been entrapped as they ventured onto the water.

6f5. Discussion

Cause of Death

The death of the birds at Rancho La Brea was due to the asphalt. Once the bird was entrapped it died either through starvation, or by poisoning as it tried to clean its plumage, or through attack by other predators. The Rancho La Brea deposit is rare in that it is possible to determine cause of death.

Biostratinomy

A study of the state of the bird bones from La Brea supports the conclusions (Sutcliffe, 1986) that little/no transport has taken place (Figure 6.21). 64% of the bones (n = 199) are unbroken and pristine compared with only 21 % (n = 1242) from an environment where transport is known to have occurred (Seymour Island, Chapter 6e). From the avifaunal analysis 67% of the birds (Table 6.8), and nearly 90% of the mammal fauna are predators/scavengers (Stock, 1956). Thus it is likely that a significant proportion of the remaining bones (the 36% broken) were damaged by scavengers/predators.

It is impossible to assess disarticulation rates and morphological decay stages because the specimens are collected as individual bones and not as articulated specimens (even if the specimens were articulated within the asphalt deposits). Nonetheless it is evident from Figure 6.21 that disarticulation occurred. For example, the radius (skeletal element category 8: Figure 6.21) is not represented; its absence indicates that disarticulation has taken place. These elements must have been removed by transport or scavenging. As it has been shown that little/no transport has taken place,

scavenging is the likely explanation (and is consistent with the high proportion of scavengers/predators in the fauna).

Preservation

The bones from Rancho La Brea are still the original apatite and show no evidence of diagenetic alteration. They are dark brown in colour due to impregnation with asphalt which has penetrated the surface and spongy parts of the bone. The bone organics have presumably decayed away. The conditions of the asphalt "trap" should be ideal for the preservation of soft tissues. The fact that the only insect chitin (of scavenging beetles e.g. *Hydrophilidae*) has been recovered is probably due to the high rates of scavenging and slow rates of burial (Sutcliffe, 1986, stated that insect evidence showed that burial did not occur for up to seven months).

Summary

Over 4130 specimens of fossil bones have been recovered from Rancho La Brea. The avifauna is very similar in diversity to comparable modern day environments. The avifauna is however biased towards predatory/scavenging birds (67% of the number of specimens). This is due to these birds being attracted to already trapped animals. The specimens are recovered as isolated well preserved bones.

6g. The Fossil Record of Birds: Completeness

The fossil record of birds is not as depauperate as most palaeo-ornithologists regard it to be (pers. comm., D. Unwin, 1994). The fossil record is, however, biased. This bias is created by differing preservation potentials of the environments that the birds inhabited. The modern avifaunas of the British Isles and Australia provide an illustration. The 221 species of British birds and 629 species of Australian birds can be divided into four main environmental categories (Table 6.9): marine, coastal, inland water (fluviatile and lacustrine), and terrestrial.

Of these four environments only totally marine and inland water have a high potential for incorporation into the geological record. Therefore only 25.8% (n=221) of British bird species and 22.5% (n=629) of Australian bird species, i.e. the taxa that inhabit these environments, are likely to be preserved as fossils.

This approach to considering bias can also be tested using the fossil record. Rich (1991) presented data on the complete Australian, Pre-Quaternary, fossil record of birds. Rich's (1991) data are used because they represent the only suitable, comprehensive source available. These data can be condensed and re-interpreted (Table 6.10). From these data it is apparent that fluviatile and lacustrine sediments preserve the majority of fossil taxa (95.3 %, n=106). Birds that inhabit inland water environments (i.e. aquatic and coastal/marine birds), as opposed to terrestrial forms, dominate inland water sediments (57.4%, n=101). Of the 43 terrestrial species found in inland water sediments 58.1 % of them are of a large size (i.e. larger than a turkey). This bias of large terrestrial birds within inland water sediments is explained by their ability to survive transportation from the terrestrial environment to the aquatic environment (Chapter 1d shows that large bones survive amounts of fluvial transport that destroy small bones). The high proportion of terrestrial taxa within the freshwater deposits can also be explained by the fact that over 25% of the modern Australian terrestrial avifauna are opportunistic nomads (Welty and Baptista, 1988) i.e. they will frequently migrate to better ecotones (the margins between different habitats) e.g. the environment around freshwater.

Using the data from Tables 6.8 and 6.9 it is possible to estimate a minimum total number of birds that must have existed before the Quaternary in Australia. If we assume that the 50 taxa that have been discovered from inland water environments equates to the complete diversity of taxa in that setting, then the minimum total number of taxa must be:

[4.1] $$50x\left(\frac{100}{18}\right) = 278$$

N.B. 18 is the percentage of aquatic birds within the modern Australian avifauna, here used as the basis for estimation (Table 6.9). Therefore the total number of taxa is 278. Therefore the maximum percentage completeness is:

[4.2] $$\frac{\text{total number of taxa discovered}}{\text{minimum total number of taxa}} \times 100 = \frac{106}{278} = 38\%$$

This approach to calculating maximum percentage completeness can be applied to the Lagerstätten described in the previous sections of this chapter. This is useful because the Lagerstätten should preserve a complete fauna and any biasing will be reflected in the maximum percentage completeness calculation. For example, there are 3 aquatic taxa within the 8 described from the Green River Formation. It can be estimated that the maximum percentage completeness is 100% (using data for the modern avifauna of Louisiana, Table 6.11, minus the passeriform birds because these had not evolved by the Eocene). The main taxa in the Green River Formation (Table 6.3) (i.e. 35.8% of the estimated total) are the Steatornithidae and Primobucconidae. These are terrestrial taxa but they are presumably preserved because, like the modern examples of these families, they inhabit the ecotones surrounding lakes.

The La Meseta Formation has a maximum percentage completeness value of 85%. This is estimated on the basis that all the marine taxa (i.e. 18 species in the Spheniscidae, Sulidae, and Pseudodontornithidae families) are represented and also using the modern sub-Antarctic avifauna (Table 6.11). The remaining taxa are terrestrial and aquatic species that have been transported into this deposit.

The asphalt deposits of Rancho La Brea have a maximum percentage completeness value of 59%. This is estimated on the basis that all the terrestrial taxa (i.e. 26) are represented and using the modern Oregon avifauna (Table 6.11). The remainder of this avifauna is made up of aquatic birds (Table 6.8).

These estimates indicate that the avifaunas of Lagerstätten are more complete (or at least are better at preserving certain type of information, such as soft tissues) than those of "normal deposits", but that they incorporate strong environmental biases, moderated by controls on transport from the surrounding area.

Rich (1991) emphasized the critical role of proximity to a depositional environment in determining which avian taxa are represented in the fossil record.

> ..... The kinds of depositional environments also determine the kinds of animals that will be preserved - namely those that lived close to the environments where deposition was occurring. In the Tertiary sites of central Australia, for example, waterbirds are by far the most common. Ducks, flamingoes, rails and charadriiforms are far more common than are pigeons and parrots. This probably bears no relationship to the actual proportions of species that inhabited and died in central Australia 10 to 20 million years ago. It is, however, related to the probability that birds living, feeding, and nesting near or in rivers or lakes are more likely to die there and to be preserved than those living elsewhere. Because of such biasing factors, one should always be cautious of interpreting low representation or absences. For example, both the parrots and the pigeons have a very dismal record in the Tertiary of Australia. In this case, the fossil record should not be used as evidence of a fairly recent radiation or invasion of the Australian continent by either of these groups. Rather, there is the real possibility that low numbers are directly related to the non-fluviatile and non-lacustrine habitats that these birds prefer. (Rich, 1991, p. 732-734).

This statement must be heeded by all palaeo-ornithologists because the taphonomy and palaeoecology of fossil birds must not be ignored or treated as a sub-standard sister to taxonomy if we are ever to dispel Olson's (1985) statement that the fossil record is poor because bird bones do not preserve.

Morphological Decay Stage	Green River Formation	Grube Messel	Solnhofen Lithographic Limestone	Seymour Island
1	7%	7%	29%	0%
2	17%	26%	42%	0%
3a	12%	22%	0%	0%
3b	14%	15%	0%	0%
3c	24%	19%	0%	0%
3d	12%	4%	0%	0%
3e	2%	2%	29%	0%
3f	5%	2%	0%	0%
3g	5%	0%	0%	0%
4	0%	2%	0%	10%
5	2%	1%	0%	90%
n =	42	124	7	1242

TABLE 6.1 **Percentages of fossil birds from four Lagerstätten corresponding to the morphological decay stages defined in Chapter 2b4.**

Aves

Neornithes

Palaeognathae

Struthioniformes	
Palaeotididae	(Early Ostriches)

Neognathae

Falconiformes	
Uncertain	
Accipitridae	(Hawks)
Galliformes	
Uncertain	
Uncertain	
Plataleidae	(Ibises)
Gruiformes	
Diatrymidae	(Cursorial, predatory birds)
Phorusrhacidae	(Flightless, predatory birds)
Cariamidae	(Seriemas)
Messelornithidae	("Messel rails")
Charadriiformes	
Phoenicopteridae	(Flamingos)
Strigiformes	
Palaeoglaucidae	(Fossil owls)
Caprimulgiformes	
Uncertain	
Apodiformes	
Aegialornithidae	(Extinct swifts)
Coraciiformes	
Coraciidae?	(True Rollers)
Atelornithidae?	(Ground Rollers)
Uncertain	
Piciformes	
Capitonidae?	(Barbets)
Uncertain	

TABLE 6.2 **Faunal list of bird species from Eocene Lake Messel (from Peters, 1992). No data are available on the numbers of each family.**

Aves

Neornithes

Neognathae

Pelicaniformes		
Fregatidae	(Frigate birds)	(1 genus, 1 species)
Galliformes		
Gallinuloididae	(Primitive moorhens)	(1 genus, 1 species)
Messelornithidae	("Messel rails")	(1 genus, 1 species)
Caprimulgiformes		
Steatornithidae	(Oilbirds)	(1 genus, 1 species)
Piciformes		
Primobucconidae	(Primitive puffbirds)	(2 genera, 4 species)

TABLE 6.3 **Avifaunal list for the Eocene, Green River Formation, Wyoming (after Grande, 1984; Unwin, 1993).**

Pterosaur species	Diet	Nos. of Specimens
Rhamphorhynchus sp. (5 species)	Piscivore	108+
Odontorhynchus aculeateus	?	?
Scaphognathus crassirostris	Piscivore	2
Anurognathus ammoni	Insectivore	1
Pterodactylus sp. (7 species)	Insectivore	60+
Gallodactylus suevicus	Piscivore	2
Germanodactylus cristatus	Piscivore	1
Germanodactylus rhamphastinus	Piscivore	3
Ctenochasma procristata	Filter	1
Ctenochasma gracile	Filter	6
Gnathosaurus subulatus	Filter	2

TABLE 6.4 **Pterosaur species of the Solnhofen Limestone with diet and number of known specimens (primary data from Wellnhofer 1990).**

Aves

Neornithes

Neognathae

Sphenisciformes		
Spheniscidae	(Penguins)	(1233 specimens)
Pelecaniformes		
Pseudodontornidae	(Marine "toothed" birds)	(2 specimens)
Sulidae?	(Boobies/Gannets)	(1 specimen)
Gruiformes		
Gruidae?	(Cranes)	(2 specimens)
Phororhacidae	(Flighless, predatory birds)	(1 specimen)
Otididae?	(Bustards)	(2 specimens)
Indeterminate to Order Level		(2 specimens)

TABLE 6.5 **Avifaunal list for the Eocene La Meseta Formation, Seymour Island, Antartica (pers. obs.).**

Genera	Species
Palaeeudyptes	*seymourensis* *marplesi* *gunnari* *antarcticus* *simpsoni*
Anthropornis	*nordenskjoeldii* *grandis*
Delphinornis	*larsenii*
Wimanornis	*seymourensis*
Ichthyopteryx	*gracilis*
Archaespheniscus	*wimani*
Orthopteryx	*gigas*
Aptenodytes	sp.
Gen. Nov.	sp. 1 sp. 2

TABLE 6.6 **List of the Spheniscidae of La Meseta Formation, Eocene, Seymour Island, Antarctica (based on Simpson, 1971 and pers. obs.).**

Aves

Neornithes

Neognathae

Sphenisciformes		
Spheniscidae	(Penguins)	(7 species)
Procellariiformes		
Diomedeidae	(Albatrosses)	(4 species)
Procellariidae	(Shearwaters/Petrels)	(23 species)
Hydrobatidae	(Storm Petrels)	(4 species)
Pelecanoididae	(Diving Petrels)	(2 species)
Pelecaniformes		
Phalacrocoracidae	(Cormorants)	(1 species)
Anseriformes		
Anatidae	(Ducks)	(1 species)
Charadriiformes		
Chionididae	(Sheath bills)	(2 species)
Stercorariidae	(Skuas)	(2 species)
Laridae	(Gulls/Terns)	(4 species)

TABLE 6.7 **Avifaunal list for the present-day Antarctic region (primary data from Fothergill, 1993).**

Aves

Neornithes

Neognathae

Podicipediformes		(2 specimens)
Podicipedidae	(Grebes)	(1 genus, 1species)
Cicconiformes		(53 specimens)
Ardeidae	(Herons)	(1 genus, 1 species)
Cicconidae	(Storks)	(1 genus, 1 species)
Anseriformes		
Anatidae	(Ducks/Geese)	(2 genera, 2 species)
Falconiformes		(2570 specimens)
Cathartidae	(Vultures)	(3 genera, 3 species)
Accipitridae	(Eagles/Hawks)	(8 genera, 8 species)
Falconidae	(Caracaras/Falcons)	(3 genera, 3 species)
Galliformes		(645 specimens)
Phasianidae	(Quails)	(1 genus, 1species)
Meleagrididae	(Turkeys)	(1 genus, 1 species)
Gruiformes		(33 specimens)
Gruidae	(Cranes)	(1 genus, 1 species)
Charadriiformes		(85 specimens)
Charadriidae	(Curlews/Snipe)	(2 genera, 2 species)
Recurvirostridae	(Avocets)	(1 genus, 1 species)
Columbiformes		(31 specimens)
Columbidae	(Pigeons/Doves)	(2 genera, 2 species)
Cuculiformes		(16 specimens)
Cuculidae	(Road Runners)	(1 genus, 1 species)
Strigiformes		(305 specimens)
Strigidae	(Owls)	(2 genera, 2 species)
Piciformes		(20 specimens)
Picidae	(Woodpeckers)	(1 genus, 1 species)
Passeriformes		(370 specimens)
Alaudidae	(Larks)	(1 genus, 1 species)
Laniidae	(Shrikes)	(1 genus, 1 species)
Corvidae	(Crows)	(2 genera, 2 species)

TABLE 6.8 **Avifaunal list for the Pleistocene deposits of Rancho La Brea (after Stock, 1956 and pers. obs.).**

LOCALITY	BRITAIN		AUSTRALIA	
ENVIRON.	NOS. OF SPECIES	% OF TOTAL AVIFAUNA	NOS. OF SPECIES	% OF TOTAL AVIFAUNA
Marine	10	4.6%	28	4.5%
Coastal	50	22.6%	94	14.9%
Inland Water	47	21.2%	113	18.0%
Terrestrial	114	51.6%	394	62.6%
Total	221	100%	629	100%

TABLE 6.9 **Numbers of British and Australian bird species classified according to environment inhabited. (N.B. 1. No rare species assessed; 2. Birds assigned to dominant habitat) (data from Gooders, 1987 and Pizzey & Doyle, 1991).**

Sedimentary environment	Abundance of material	Nos. of coastal and marine taxa	Nos. of terrestrial Taxa	Nos. of aquatic taxa	Total nos. of taxa
Terrestrial	Absent	0	0	0	0
Inland Water	>300 bones	8	43	50	101
Coastal and Marine	<100 bones	5	0	0	5

TABLE 6.10 **The complete fossil record of Australian birds differentiated into their ecological habits compared with the sedimentological setting in which they were found, (after Rich, 1991).**

FIGURE 6.1 An unidentified bird (FMNH PA607) from the Eocene, Green River Formation, Wyoming. The specimen appears to have "bypassed" morphological decay stages 3a and 3b and has reached stage 3c, i.e. disarticulation of the pectoral girdle from the thorax has occurred before disarticulation of the skull from the cervical vertebrae, and the legs from the synsacral articulation.


INCHES
Cat. M1075
Baxter
Scientific Products
METRIC 1 2 3 4 5 6 7 8

FIGURE 6.2 The holotype specimen of *Primobucco olsoni* (GSATC 217) from the Eocene, Green River Formation of Wyoming. This fossil specimen corresponds to the experimental morphological decay stage 1. The bird is fully articulated and shows the preservation of feathers/soft tissues around the body.

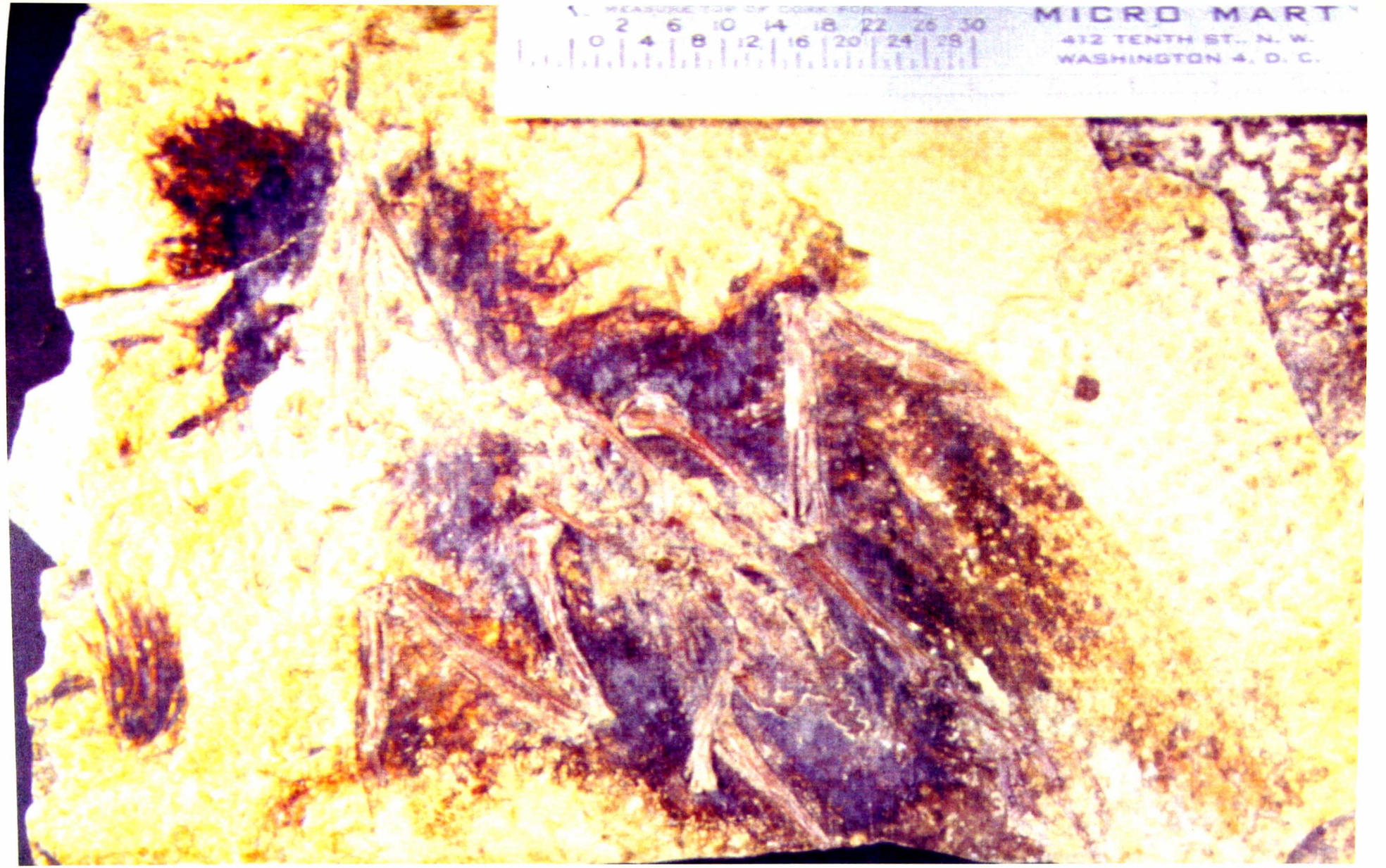

MICRO MART
412 TENTH ST., N. W.
WASHINGTON 4, D. C.

FIGURE 6.3 An undescribed specimen of bird (USNM 336268) from the Eocene, Green River Formation of Wyoming. The specimen corresponds to the experimental morphological decay stage 2. The bird is fully articulated but no feathers/soft tissues are present.


INCHES
MEASURE TOP OF CORK FOR SIZE
2 6 10 14 18 22 26 30
0 4 8 12 16 20 24 28
METRIC
MICRO MA
412 TENTH ST., N.
WASHINGTON 4, D.

FIGURE 6.4 The holotype specimen of *Pseudocrypturus cercanaxius* (USNM 336103) from the Eocene, Green River Formation of Wyoming. The specimen corresponds to the experimental morphological decay stage 3a. The skull has separated from the body due to the disarticulation of the cervical vertebrae.


INCHES
MEASURE TOP OF CORK FOR SIZE
2 6 10 14 18 22 26 30
0 4 8 12 16 20 24 28
METRIC
MICRO MART
412 TENTH ST., N. W.
WASHINGTON 4, D. C.

FIGURE 6.5 Undescribed species of bird (USNM 336264) from the Eocene, Green River Formation of Wyoming. The specimen corresponds to the experimental morphological decay stage 3b. The legs have disarticulated from the synsacral articulation.


INCHES
MEASURE TOP OF CORK FOR SIZE
2 6 10 14 18 22 26 30
0 4 8 12 16 20 24 28
METRIC
MIC
412 T
WASH

FIGURE 6.6 An unidentified bird (GMUW V80102-20313) from the Eocene, Green River Formation of Wyoming. The specimen corresponds to the experimental morphological decay stage 3c. The pectoral girdle has disarticulated from the thorax.

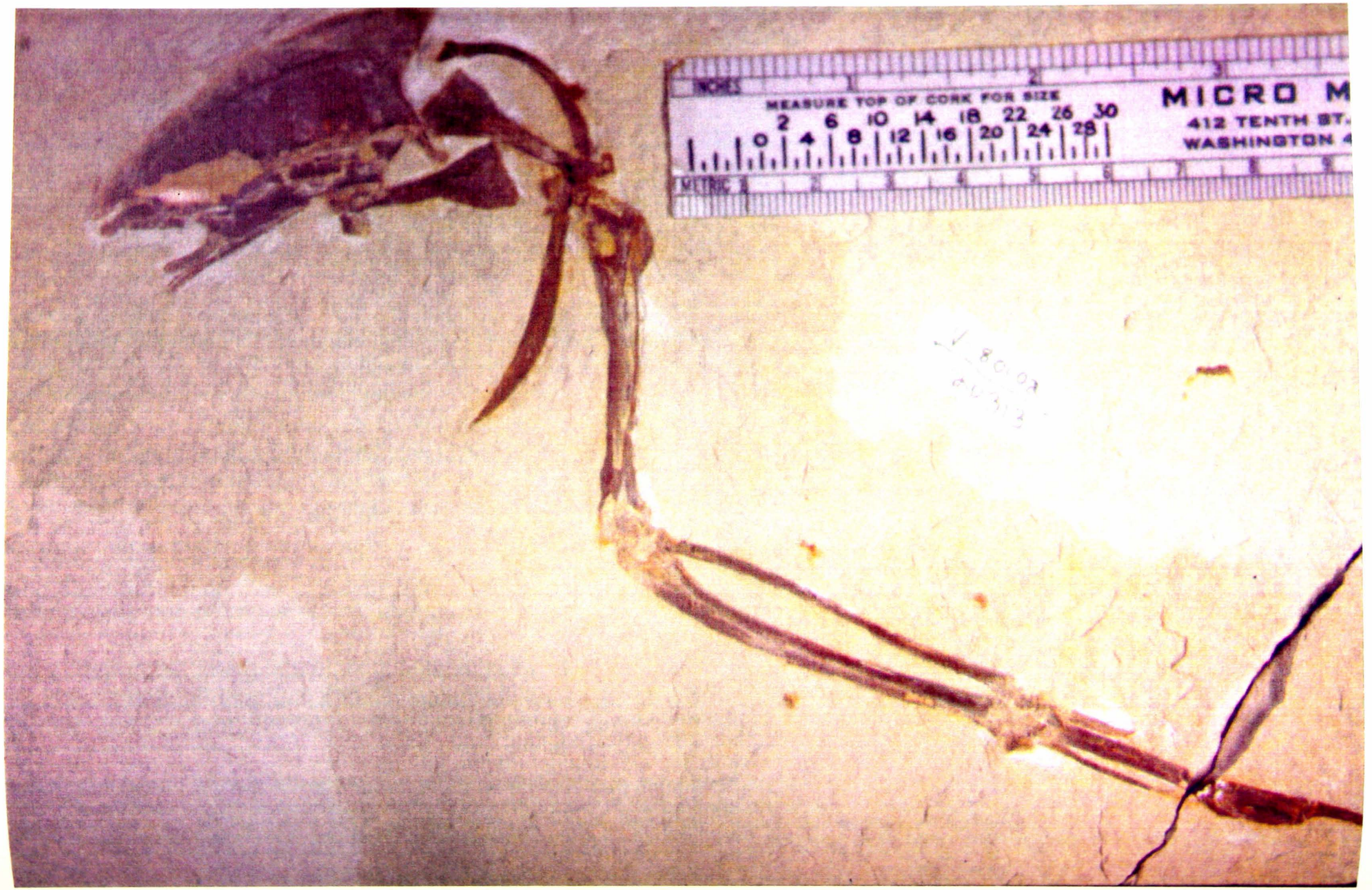

INCHES
MEASURE TOP OF CORK FOR SIZE
2 6 10 14 18 22 26 30
0 4 8 12 16 20 24 28
MICRO M
412 TENTH ST.
WASHINGTON

FIGURE 6.7 The paratype specimen of *Limofregata azygosternon* (USNM 243766) from the Eocene, Green River Formation of Wyoming. The specimen corresponds to the experimental morphological decay stage 5. The specimen is totally disarticulated and shows damage caused by external factors.


MEASURE TOP OF CORK FOR SIZE
2 6 10 14 18 22 26 30
0 4 8 12 16 20 24 28

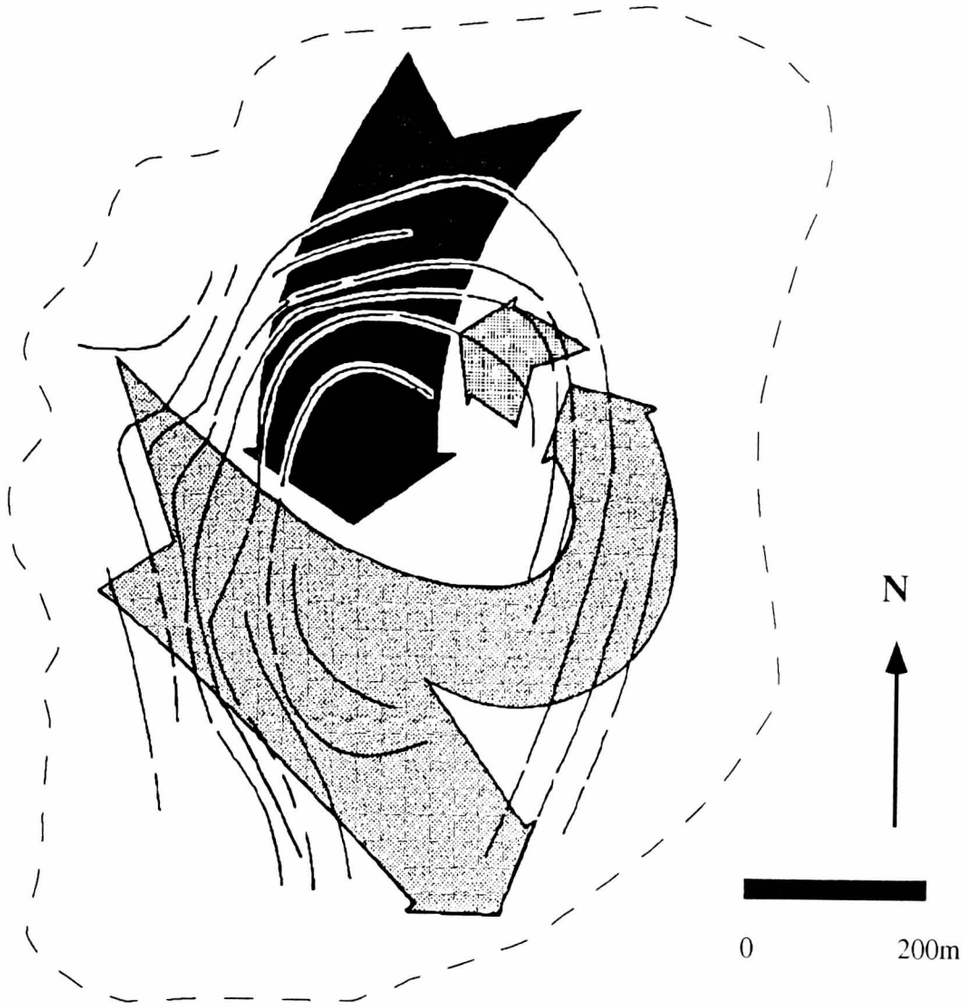


FIGURE 6.8 Reconstruction of flow directions in Lake Messel. Directional data taken from measurements on fossil fish. Black continuous lines are reconstructed isobaths (contours of equal depths). Dotted lines indicate present extent of Grube Messel. Arrows show flow directions and two inlets (North and North-West) and one outlet (South-East). Adapted from Schaal (1992).

Figure 6.9 Graph of % of fossil birds from Grube Messel in each morphological decay stage.

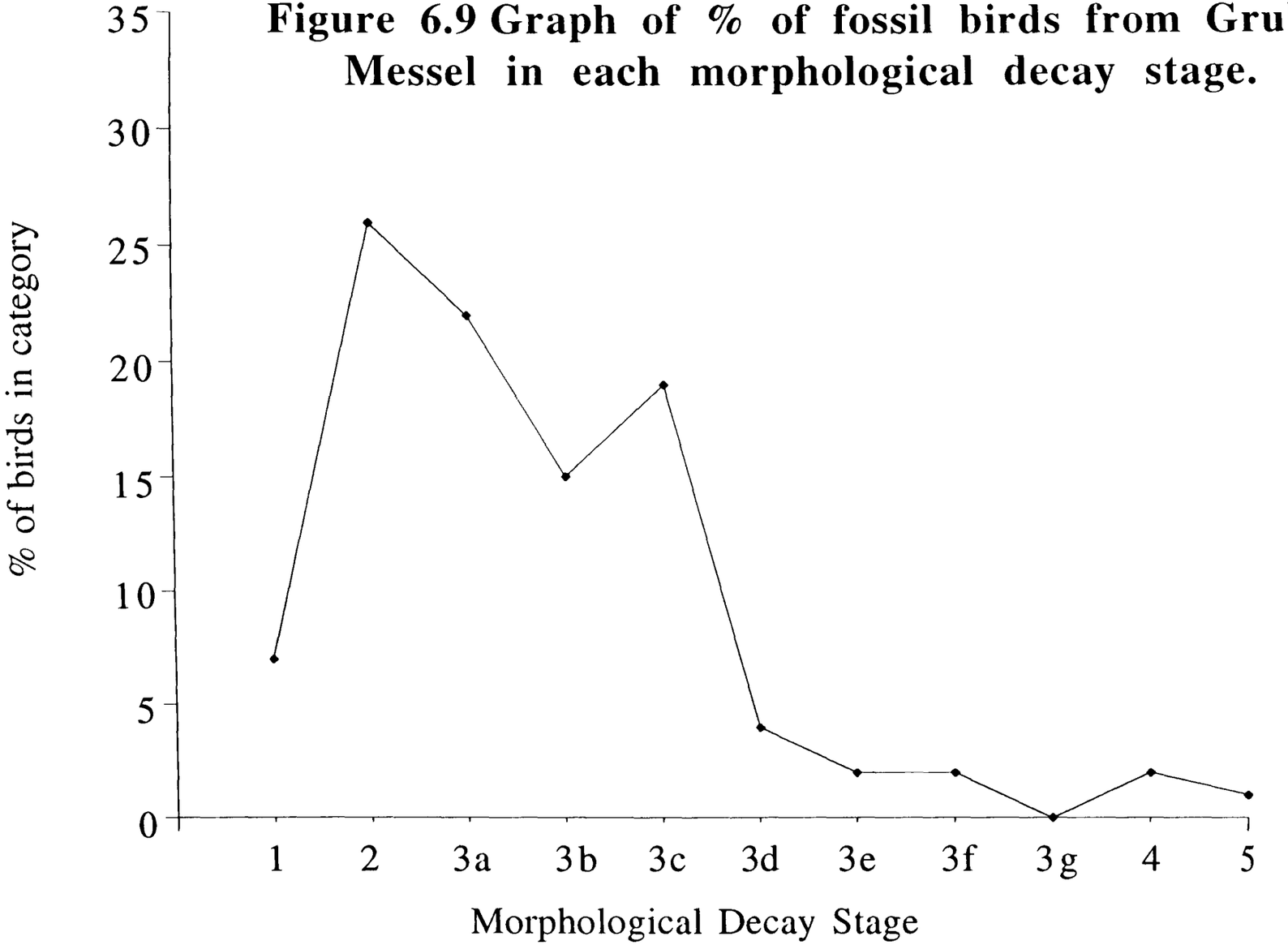
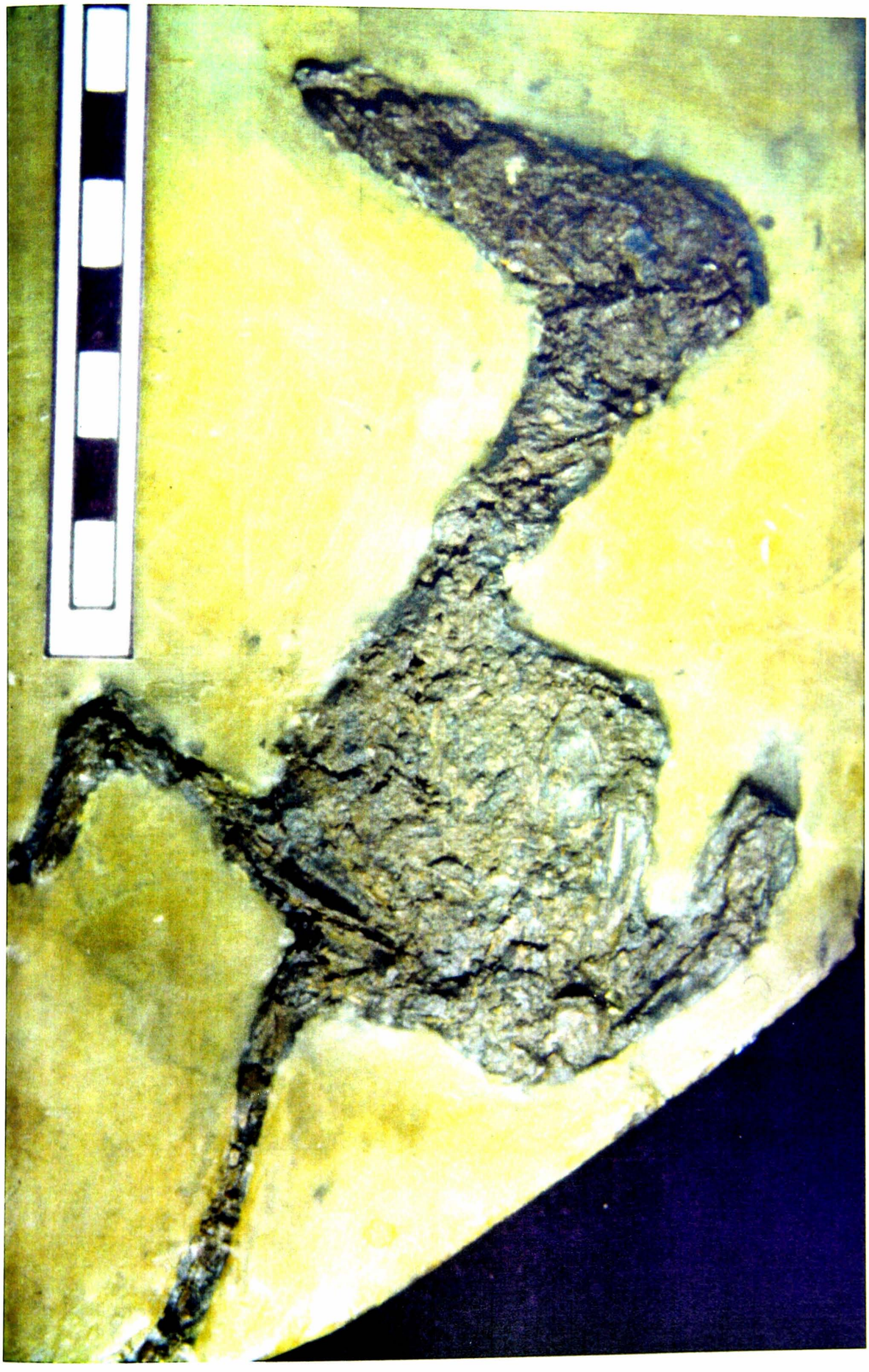


FIGURE 6.10 An unidentified bird from Grube Messel (HLMD gef 1950) showing a "mushy skeleton". The specimen is completely crushed and diagenetic porewaters have precipitated phosphate onto the broken bones of the skeleton. These specimens preserve little anatomical information but yield important data on bird abundances and taphonomy.



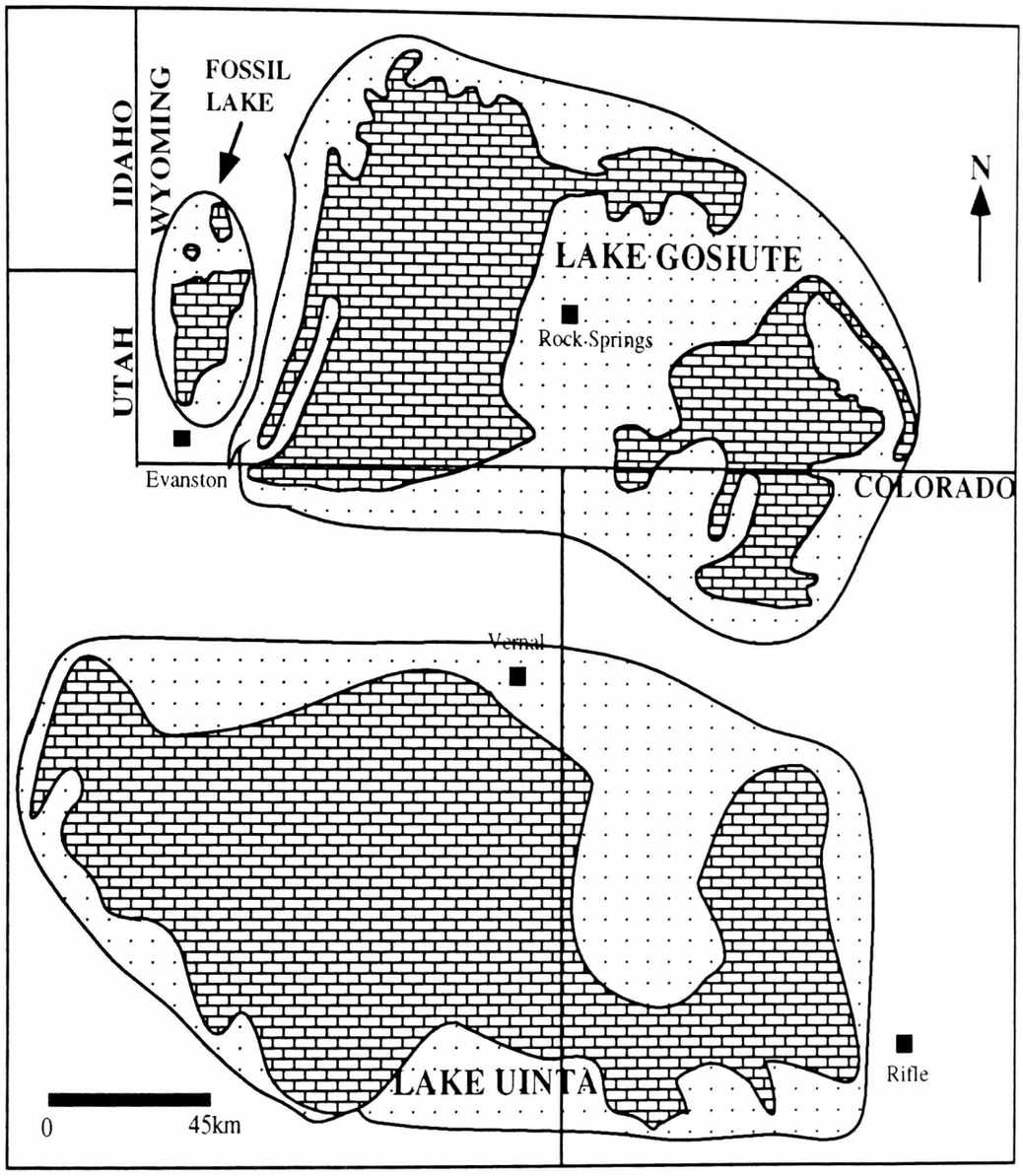


FIGURE 6.11 **The outcrop and maximum extent of the Green River Formation (adapted from Grande, 1984).**

Figure 6.12 Graph of % of fossil birds (n=42) from the Green River Formation in each morphological decay stage.

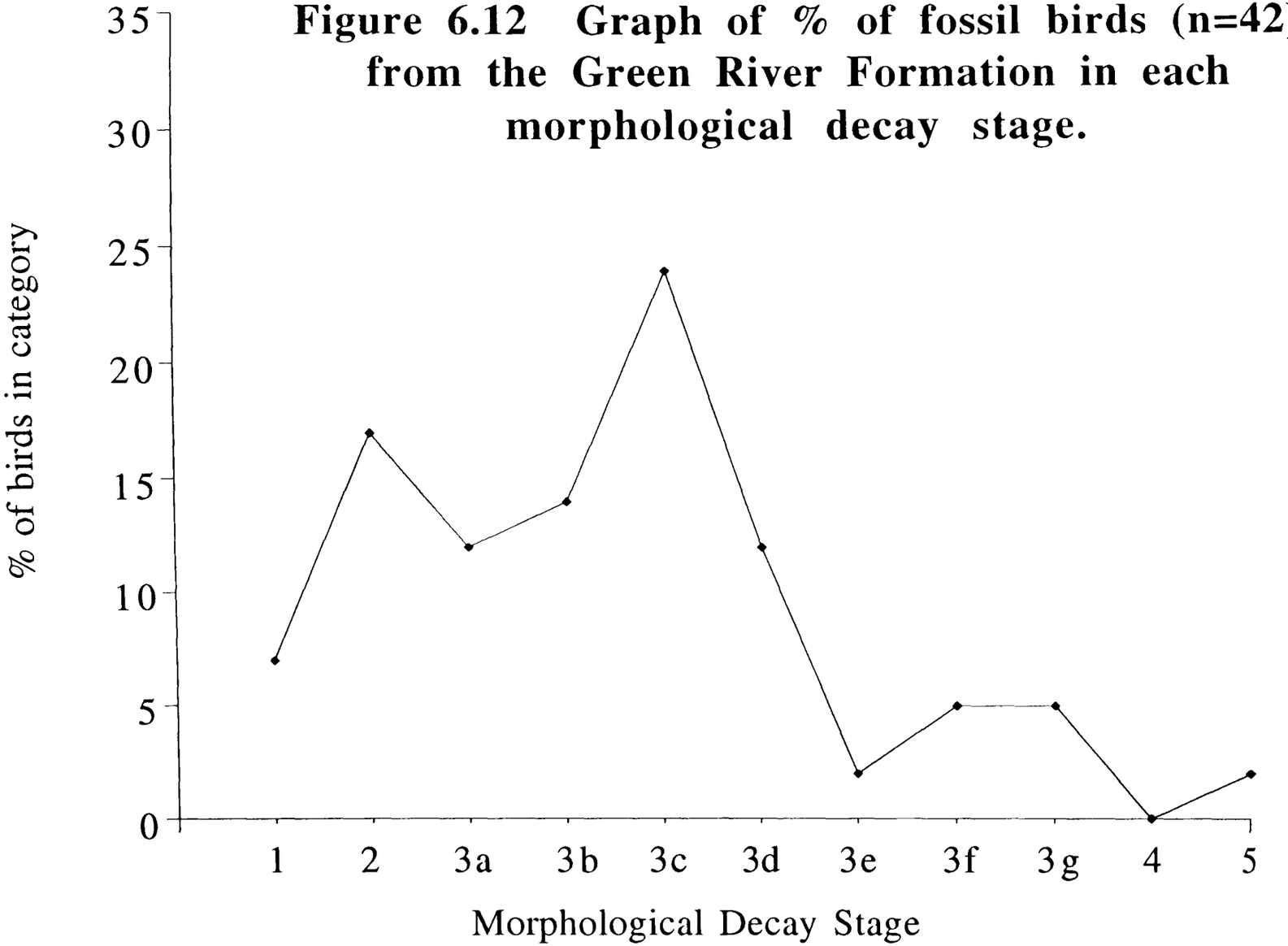
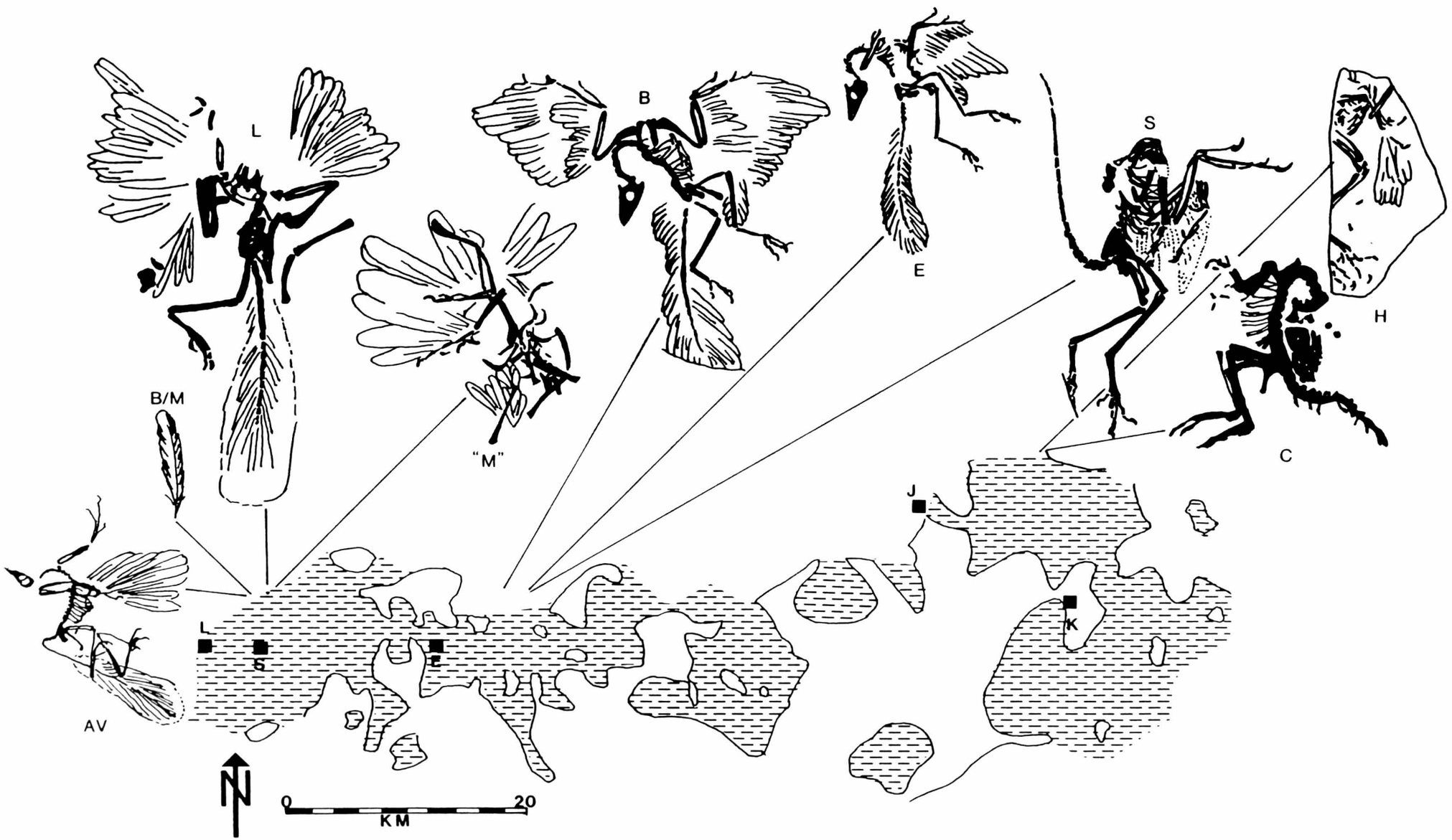


FIGURE 6.13 Geological map of the Solnhofen area with the discovery localities of *Archaeopteryx* and *Compsognathus* marked on. Disarticulation of the specimens increases from East to West. The outcrop of Solnhofen Lithographic Limestone is indicated by dashed fill. L = Langenaltheim, S = Solnhofen, E = Eichstätt, J = Jachenhausen, K = Kelheim. AV = Aktein-Vereins specimen, B/M = Berlin/Munich feather, L = London specimen, B = Berlin specimen, E = Eichstätt, S = Solnhofen specimen, C = *Compsognathus*, H = Haarlem specimen (adapted from Wellnhofer, 1988a).


L
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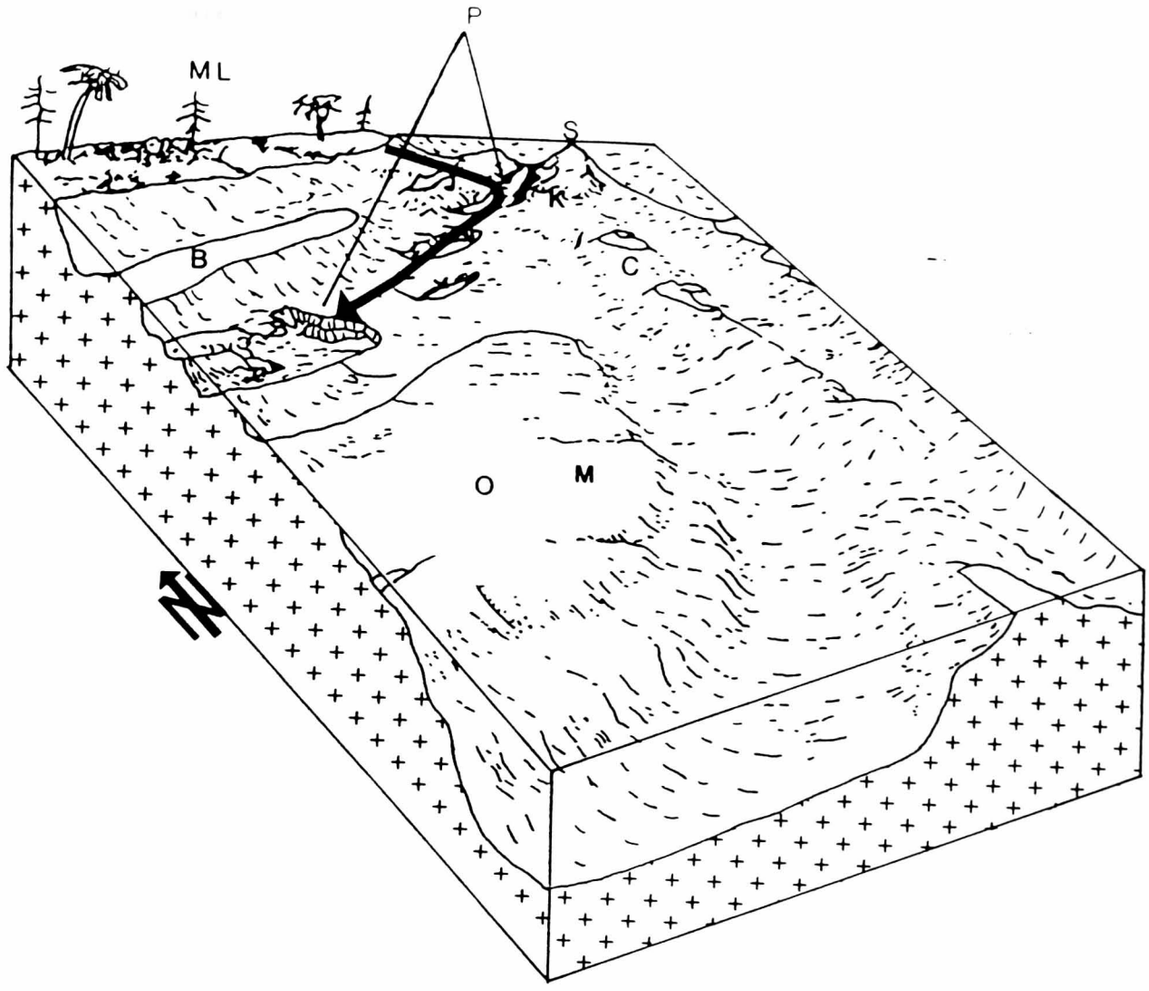
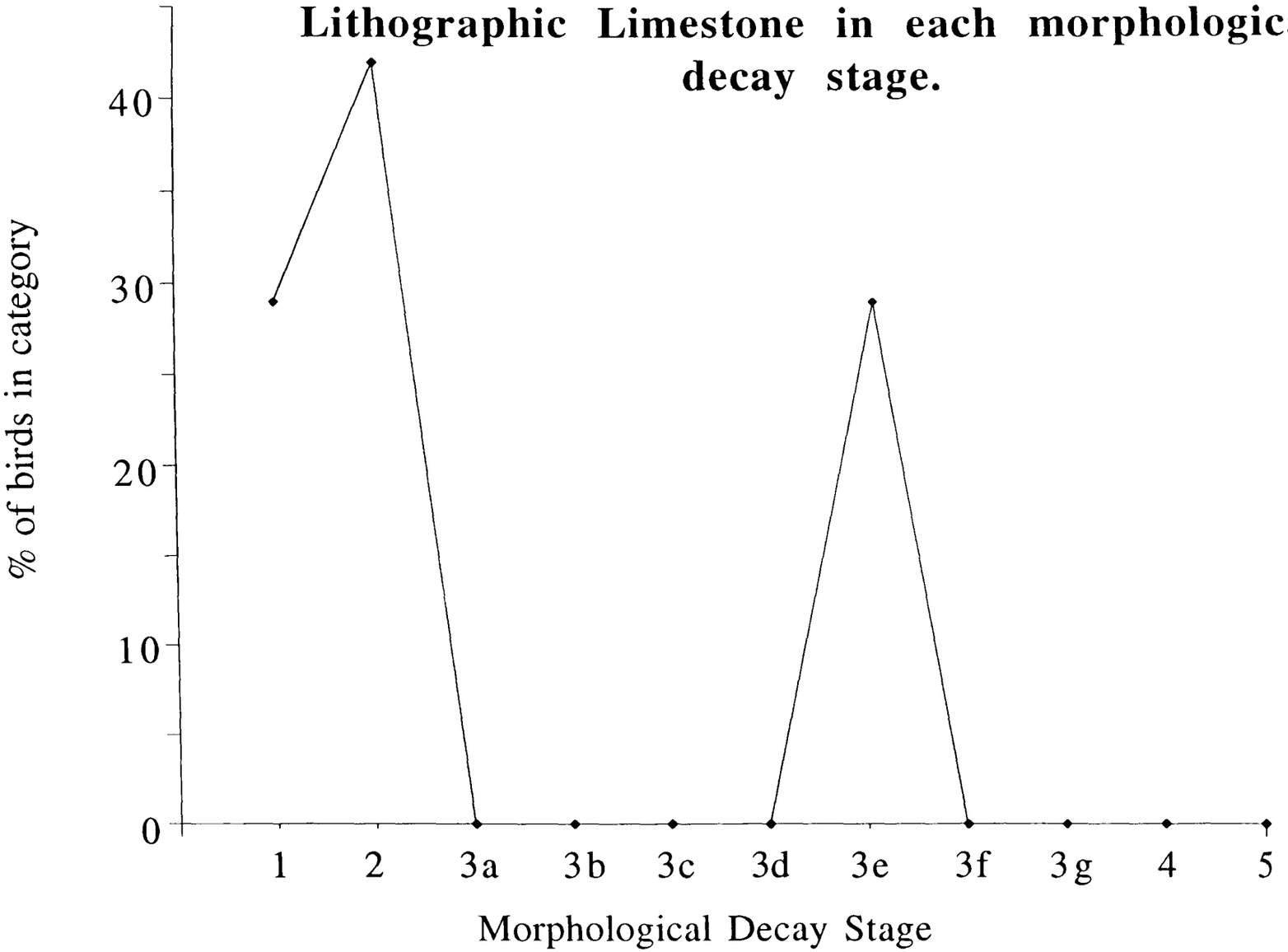


FIGURE 6.14 Palaeogeography of the Solnhofen area. Arrow shows possible direction of transport for *Archaeopteryx* and *Compsognathus* specimens. Direct transport from the westerly Plattenkalk basin was prevented by a barrier, possibly a coral reef/sponge mound/ooid shoal. ML = Middledeutsch landmass. B = barrier. P = Plattenkalk basin. O = ooid shoal. S = sponge mound. C = coral reef. K = Kelheim. M = Munich. S = Solnhofen (adapted from Bartel *et al.*, 1990).

Figure 6.15 Graph of % of fossil birds from Solnhofen Lithographic Limestone in each morphological decay stage.



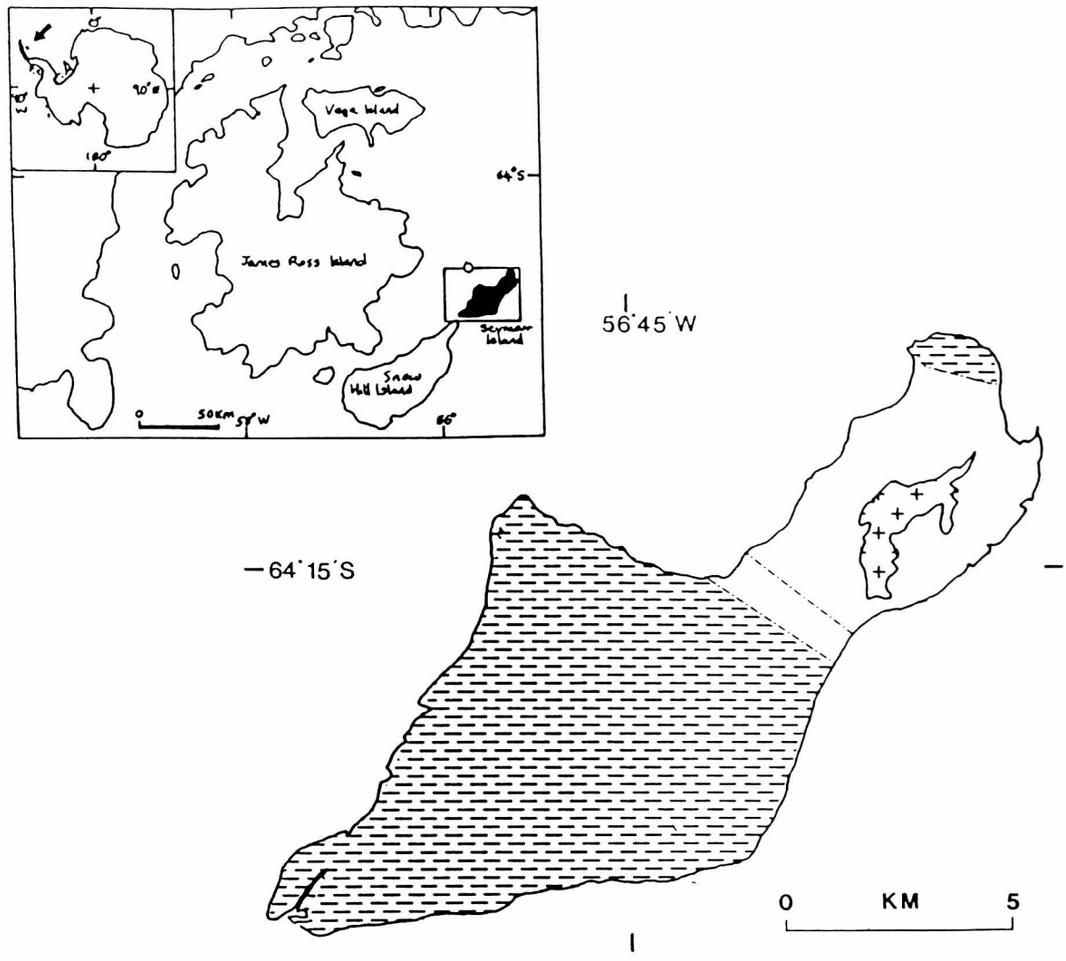


FIGURE 6.16 Geological map of Seymour Island (adapted from Elliot *et al.*, 1975). Dotted lines indicate faults; crosses indicate Quaternary sediments; white fill indicates the La Meseta Formation; dashed fill indicates Cretaceous sediments.

FIGURE 6.17 A leopard seal violently thrashing the carcass of an Adélie penguin (*Pygoscelis adeliae*) against the water. This strips the cadaver of its flesh. A leopard seal may take up to an hour to eat a penguin in this way. This type of behaviour obviously affects the rate of disarticulation of the carcass. Photograph taken by Ben Osborne and courtesy of the B.B.C. Natural History Unit.

KEY TO FIGURE 6.18

1 = Skull
2 = Vertebrae
3 = Sternum
4 = Furcula
5 = Coracoid
6 = Scapula
7 = Humerus
8 = Radius
9 = Ulna
10 = Carpometacarpus
11 = Phalanges
12 = Rib
13 = Synsacrum
14 = Femur
15 = Patella
16 = Tibiotarsus
17 = Fibula
18 = Tarsometatarsus
19 = Pes digits

Figure 6.18 Graph of % of skeletal elements in skeletal categories for the La Meseta Fm.

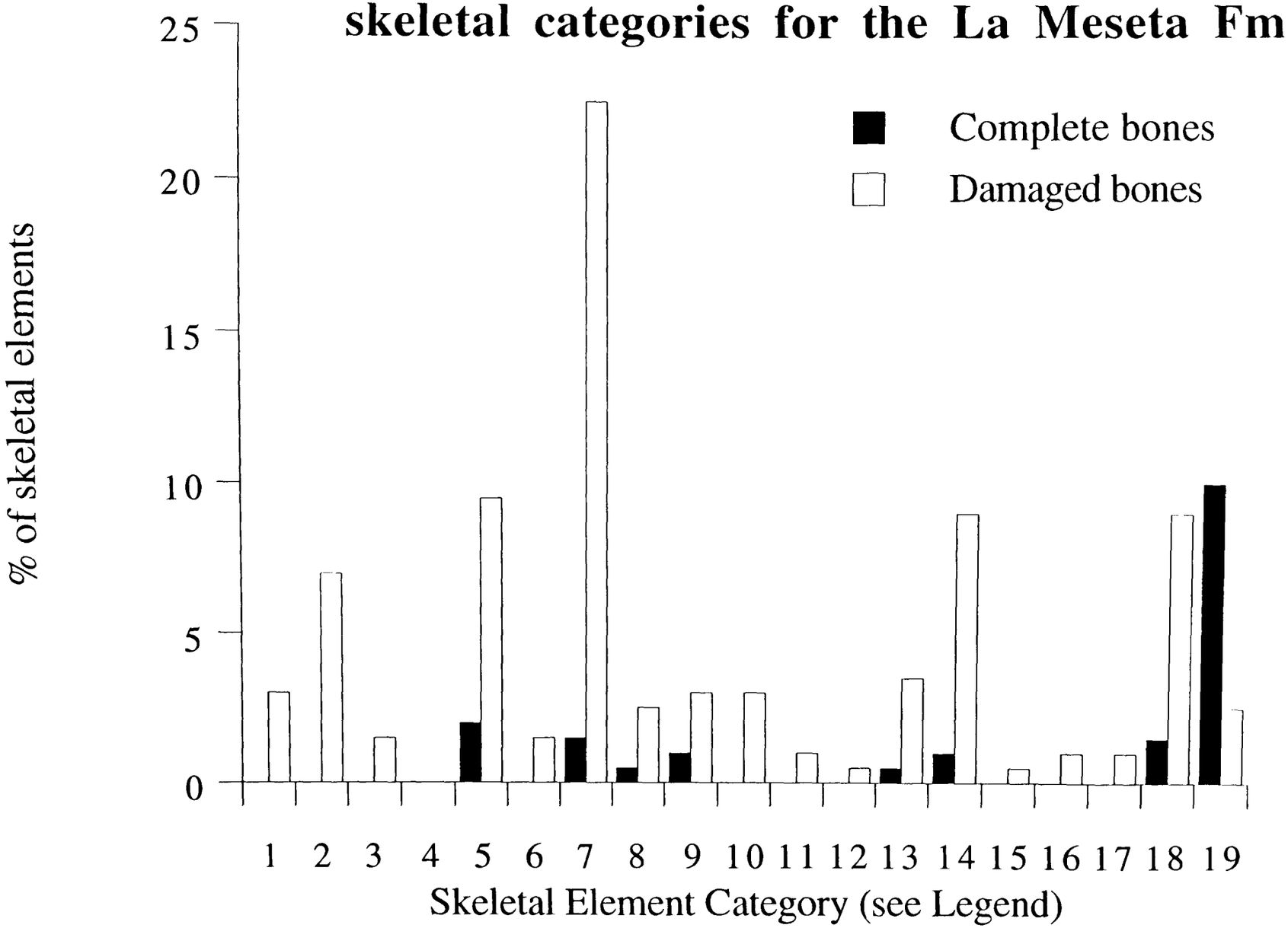
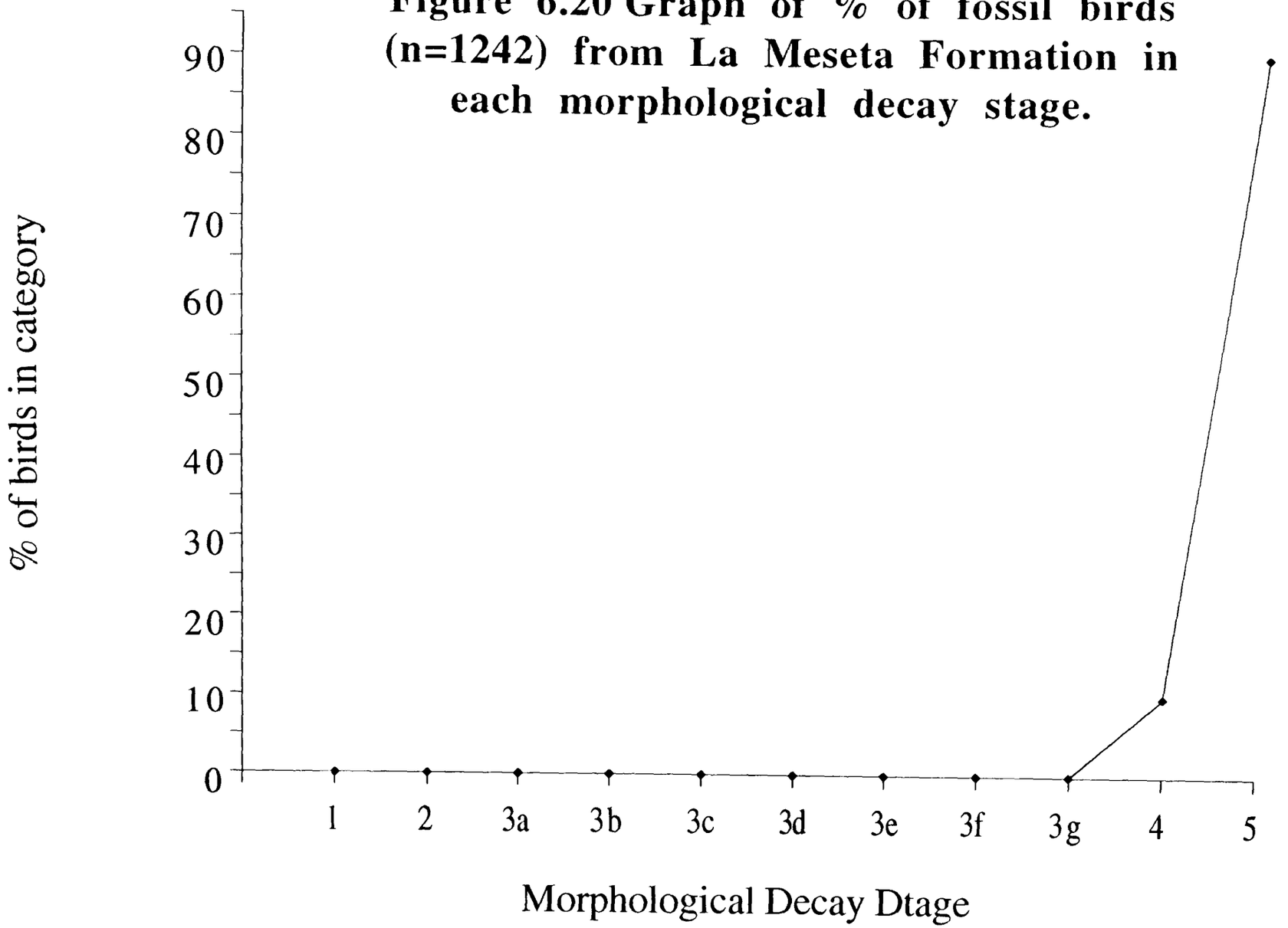


FIGURE 6.19 Giant petrels rip into an elephant seal carcass. Cape petrels wait for scraps. The pressure for food is so great within the harsh environment that scavenging becomes essential to survival (e.g. the South Georgia pintail duck is adapted to a vegetarian diet but readily eats carrion). Photograph taken by Ben Osborne and courtesy of the B.B.C. Natural History Unit.

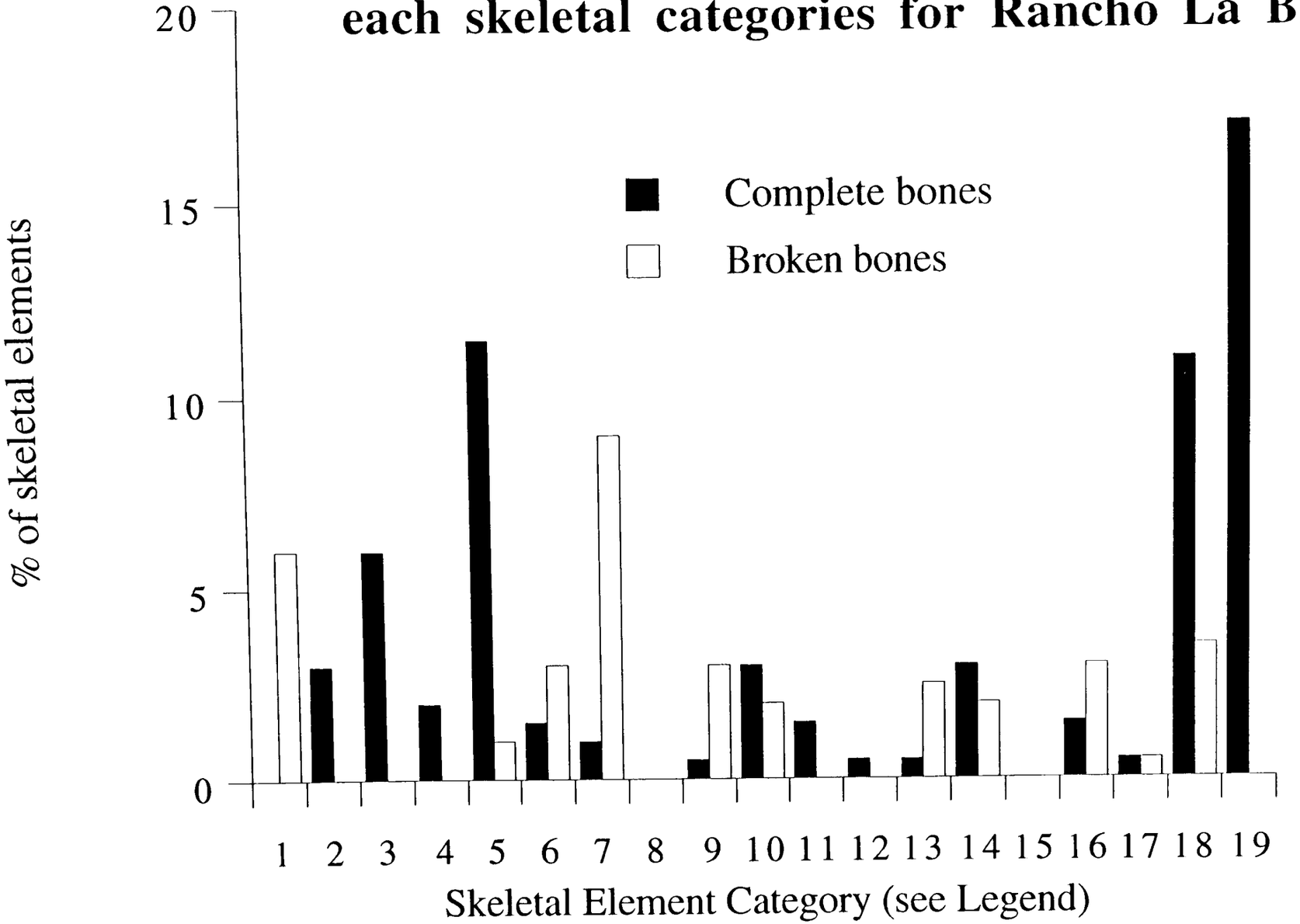
Figure 6.20 Graph of % of fossil birds (n=1242) from La Meseta Formation in each morphological decay stage.



KEY TO FIGURE 6.21

1 = Skull
2 = Vertebrae
3 = Sternum
4 = Furcula
5 = Coracoid
6 = Scapula
7 = Humerus
8 = Radius
9 = Ulna
10 = Carpometacarpus
11 = Phalanges
12 = Rib
13 = Synsacrum
14 = Femur
15 = Patella
16 = Tibiotarsus
17 = Fibula
18 = Tarsometatarsus
19 = Pes digits

Figure 6.21 Graph of % of skeletal elements in each skeletal categories for Rancho La Brea



Chapter Seven
The Taphonomy of Bats

7a. Introduction

The fossil record of bats is depauperate. Table 7.1 shows all the known fossil bat genera.

There are 26 genera and 64 species within 11 families of fossil bats, which compares with the 173 genera and 985 species within 17 families of extant forms. The depauperacy of the bat fossil record is highlighted when compared against that of birds (Figure 7.1). Why is the fossil record of bats depauperate? There are several possible explanations:

1. The fossil record is a true reflection of ancient diversity. Bats did not diversify significantly until the Pleistocene. This can be shown to be false by the diversity of bats that have been found in the Lagerstatte deposits of Grube Messel (see Chapter 7b).
2. Bats, being flying animals, are not readily preserved. The previous six chapters of this thesis have shown that flying vertebrates can, and do, preserve well. In fact, bats should have a better fossil record than birds, as they have teeth (Appendix 3, for skeletal anatomy) which have been shown to preserve very well (e.g. Shipman, 1981; Behrensmeyer and Hill, 1980; Behrensmeyer, 1991).
3. Bats inhabit areas unlikely to be preserved in the geological record. This is the most likely explanation of the paucity of the bat fossil record. Bats inhabit terrestrial areas (even though they fly above the land, they spend at least 40% of their time roosting in caves/trees etc.), and terrestrial sediments are very rarely incorporated into the geological record, the exceptions being cave, fluviatile and lacustrine sediments from which all of the fossil bat specimens have been recorded. The majority of modern species (approximately 80%, Webb *et al.*, 1977) do not inhabit fluviatile or lacustrine environments. Therefore we can conclude that habitat preference is the main cause of the paucity of the bat fossil record.

Nearly all fossil bats have been described based on teeth. Isolated bones are rare. Complete specimens have only been found in four lacustrine deposits: Green River Formation (Eocene), Grube Messel (Eocene), Geiseltal (Eocene) and the lignites of Venetia, Italy (Oligocene). Of these deposits only Grube Messel has produced fossil bats in quantity. Grube Messel has yielded over 200 specimens (they are the most common mammalian fossils); the other three deposits have only produced about 7 specimens in total.

It would be pointless here to review the work done on the taphonomy of mammalian teeth. All that is needed is to state that bat teeth are likely to behave taphonomically like other small mammalian teeth (i.e. Insectivores) (because of their similarity in structure and morphology) and to direct the reader to the voluminous literature on this subject (e.g. Shipman, 1981; Behrensmeyer and Hill, 1980; Behrensmeyer, 1991).

However, the experimental data in Chapter 2, and the large amounts of fossil material from Grube Messel (Appendix 9), allow the taphonomy of the skeleton (as opposed to teeth) of bats to be investigated and compared to that of birds.

7b. Taphonomy of the bats of Grube Messel

The sedimentology and palaeo-environment of Grube Messel are described in Chapters 6b1. and 6b2. The specimens of fossil bats from Grube Messel have been assigned to seven species (Table 7.2).

The high diversity of Chiropteran remains at Grube Messel is unusual; they are the most common mammalian fossil (Habersetzer *et al.*, 1992). Habersetzer *et al.* (1992) suggested that because most of the bats are preserved with their gastrointestinal contents, they must have died during their nocturnal hunt or shortly afterwards (as extant species quickly void any indigestible parts of their food). They also judged that the bats were healthy adults (from the wear on the teeth and the osteology of the skeletons). As the bats were in the prime of life and active shortly before their demise, they must have died an unnatural death. Habersetzer *et al.* (1992) ruled out predators (as there are no traces of their activities) and postulated that clouds of poisonous gas (as suggested by Rietschel, 1987), emitted from the lake, led to the fall and the drowning of the bats that were hunting over the surface of the water. Studies on stomach contents allowed "hunting arenas" for the different species of bats to be deduced. *Palaeochiropteryx* hunted at low levels, *Archaeonycteris* at medium levels and *Hassianycteris* hunted in the forest canopy (Figure 7.2). If the poison gas theory were correct then more specimens of low flying species (*Palaeochiropteryx*) should be present in the sediments of Grube Messel (as they would be more endangered). Habersetzer *et al.* (1992) found that this is the case as 74% of the Messel bat fauna is accounted for by *Palaeochiropteryx tupaiodon*. I discovered that 82.5% (n=57) of the identified chiropterans in the Hessisches Landesmuseum, Darmstadt are of the genus *Palaeochiropteryx*, and 70% (n=57) are of the species *P. tupaiodon*.

While the 'poison gas' theory appears to explain the abundance of chiropterans at Messel it probably does not apply to the birds (see Chapter 6b4. for reasons).

If the Chiropterans died suddenly over the lake they should, on the whole, be well preserved. Bats do not float (pers. obs.), especially when they drown and the lungs fill with water. They would have sunk rapidly to the lake bottom, which was anoxic (see Chapter 6b4. and Figure 5.4.) so protecting the carcass from scavengers. If poisonous gases were being released they would poison the water column killing scavengers (e.g. fish). If we assume that bats decay/disarticulate in the same sequence as birds (Chapter 2) then a graph of morphological decay stage versus percentage of bats in each category can be produced (Figure 7.3, data from Appendix 9). The graph shows that 48% (n=69) of the bats can be classified as morphological decay stages 1 and 2 (complete and articulated +/- soft tissues, Chapter 2). This agrees with the theory that the bats were killed quickly, fell directly into the lake, were not scavenged and are unlikely to have been transported. A peak occurs on the graph corresponding to morphological decay stage 3c: 31% (n=69) of the specimens that have been found are isolated wings or carcasses without wings. This group probably represents bats that died naturally and were transported to the lake (as described for the avifauna, Chapter 6b4.). Scavenging can be ruled out as bat carcasses are quickly and completely consumed. Observations were carried out on the decay/disarticulation of bats using the methods described for birds (Chapter 2). Five unprotected bat carcasses (*Glossophaga soricina*) were placed out within the Florida freshwater site. All of the carcasses had completely disappeared within three hours due to scavenger activity. This was attributed to racoons, *Procyon lotor*.

The soft tissue of the wings and body is preserved as an outline by bacteria auto-lithified in siderite (see Chapters 5 and 6b4.). The stomach contents, however, are not preserved in this way, but as diagenetically altered original organic material, e.g. the chitin exoskeleton of insects has just been "carbonised". The fact that soft tissues are not uncommon in the fossil bats from Messel (43%, n=69) indicates that microbial decay occurred on the lake bed rather than as the carcass descended through the water. The fossil must have been buried quickly to allow autolithification of the bacteria that we now see as the "soft tissue", probably as a result of settling out of large amounts of sediment from the water column (due to the requirement of reducing conditions for the preservation of soft-tissues, this only occurred in reducing conditions i.e. below the sediment water interface, Wuttke, 1983). This sediment was re-suspended by the large scale de-gassing of the lake bed

sediments (Rietschel, 1987) (it must have occurred on a large scale as the Chiropterans could have flown through small pockets of poison gas).

The preservation of the bone is identical to that of birds (and the other vertebrates). The bats also show the "mushy skeleton" described by Peters (1992) for the birds (Chapter 6b4). The bat specimens show a much higher proportion of this effect (23.5%, n=64) than do birds (3%, n=128). The "mushy" texture seen in the bats affects the very thin, delicate bones of the skeletons (i.e. the scapula, vertebrae, ribs, pelvis, leg elements, and the cranium). As in birds (Chapter 6b4) this texture was probably caused by precipitation of calcium phosphate on the crushed bones of the skeleton. The bats also show a further extension of this process. In some (8%, n=64) of the specimens which show the "mushy" texture the most delicate bones are absent, although it is clear that they were present at the time of burial (Figure 7.4). These most delicate bones must have been dissolved by pore waters. Only the crushed, delicate bones were affected because a basic chemical principle of dissolving substances states that smaller particles, and particles with large surface area in relation to weight, dissolve more quickly, i.e. in this case the crushed, thin walled, delicate bones of the skeleton.

The fact that dissolution and precipitation of phosphate were taking place in the diagenetic pore waters of the Messel sediments indicates that fluctuations in pH of the pore waters was occurring (see Prévôt and Lucas, 1991).

7c. Discussion

The depauperate fossil record of bats results from their occupation of unsuitable areas for fossil preservation. The record is dominated by teeth, which have been shown to be recalcitrant (e.g. Shipman, 1981; Behrensmeyer and Hill 1980; Behrensmeyer 1991). Rare skeletal material is known, but this is always from lacustrine or cave deposits (eg. Messel, Green River, numerous Pleistocene cave deposits). The study of this material (see 7b above) shows that bats undergo a similar taphonomic history to birds within the same deposit. Thus the similarities of structure in birds and bats is sufficient to result in a similar taphonomic history.

Class : Mammalia
Order :: Chiroptera (Bats)
Suborder : Megachiroptera (Fruit Bats/Flying Foxes)

		Age
Pteropidae		
Archaeopteropus	(1 species)	Oligocene

Suborder : Microchiroptera (Insect-eating bats/vampires)

Icaronycteridae		
Icaronycteris	(1 species)	Eocene
Archaeonycteridae		
Archaeonycteris	(2 species)	Eocene
Palaeochiropterygidae		
Palaeochiropteryx	(2 species)	Eocene
Cecilionycteris	(1 species)	Eocene
Hassianycteridae		
Hassianycteris	(3 species)	Eocene
Rhinolophidae		
Palaeophyllophora	(4 species)	Olig. - M. Mio.
Palaeonycteris	(1 species)	Lower Oligocene
Rhinolophus	(2? species)	M. Eocene - Recent
Hipposideridae		
Hipposideros	(11 species)	U. Olig. - L. Mio.
Megadermidae		
Necromantis	(3 species)	U. Eoc. - M. Mio.
Megaderma	(2 species)	Oligocene
Miomegaderma	(1 species)	Oligocene
Emballonuridae		
Vespertiliauus	(4 species)	U. Eoc. - L. Olig.
Vespertilionidae		
Nycterobius	(1 species)	U. Eoc. - L. Olig.
Leuconoe	(1 species)	Oligocene
Tararida	(1 species)	Oligocene
Myotis	(9 species)	Oligocene - Recent
Samonycteris	(1 species)	Upper Miocene
Simonycteris	(1 species)	Pliocene
Mystipterus	(1 species)	Pliocene
Molossidae		
Nyctinomus (sensu lato)	(2 species)	Oligocene - Recent
Molossides	(1 species)	Pleistocene
Incertae sedis		
Paleunycteris	(4 species)	Eocene - Oligocene
Paradoxonycteris	(2 species)	Eocene
"Vespertillio"	(2 species)	Eocene - Oligocene

TABLE 7.1 **List of all known fossil bat genera with numbers of species described and geological age ranges (revised from Allen, 1967).**

Class Mammalia

Order Chiroptera

Suborder Microchiroptera

Archaeonycteridae

Archaeoncteris trigonodon

Archaeonycteris pollex

Palaeochiropterygidae

Palaeochiropteryx tupaiodon

Palaeochiropteryx spiegeli

Hassianycteridídae

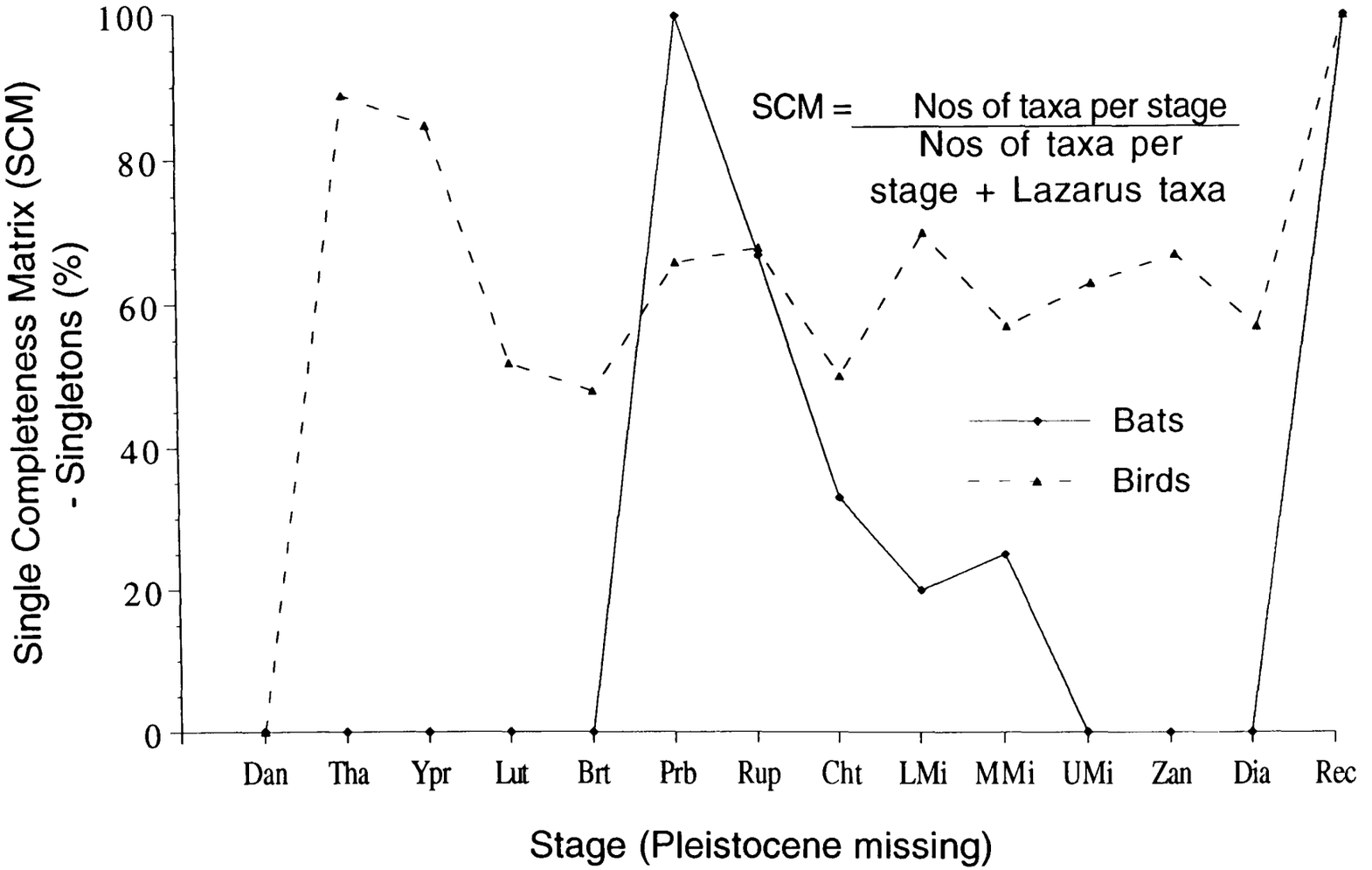
Hassianycteris messelensis

Hassianycteris magna

Hassianycteris revilliodi

TABLE 7.2 **Faunal list of the Chiroptera from the deposits of Grube Messel (Eocene), Germany (after Habersetzer *et al.*, 1992).**

Figure 7.1 Depauperacy of the fossil record of bats compared to that of birds using SCM - Singletons method.



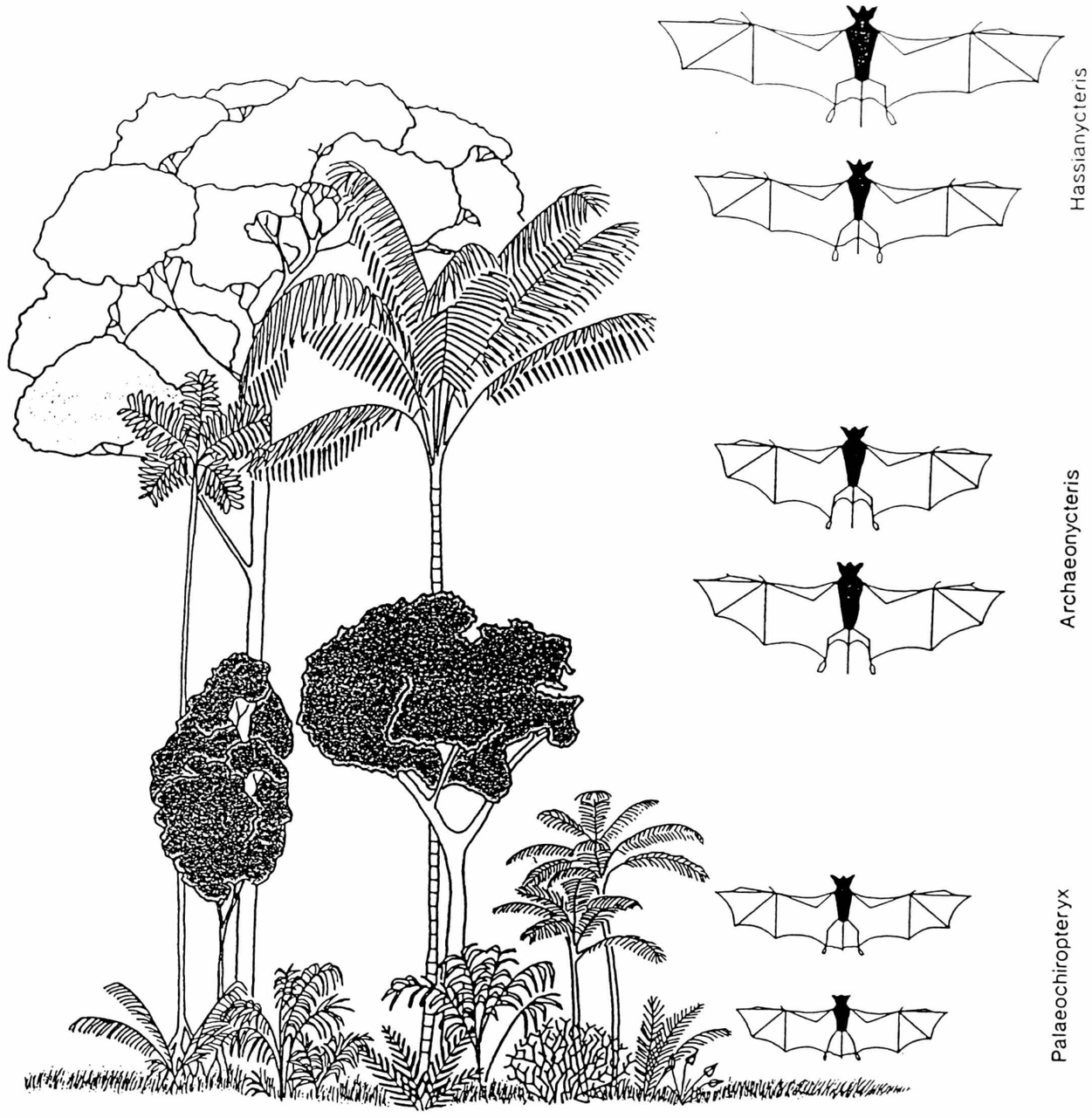


Figure 7.2 Hunting arenas for the fossil bat genera from Messel, deduced by stomach contents. *Palaeochiropteryx* with a small wing-span (ca. 25-30cm) hunted at low levels, *Archaeonycteris* with a medium wing-span (ca. 32-37cm) hunted at intermediate levels and *Hassianycteris* with a large wing span (ca. 38-48cm) hunted in the forest canopy (from Habersetzer *et al.*, 1992).

Figure 7.3 Graph of % of fossil bats (n=69) from Grube Messel in each morphological decay stage

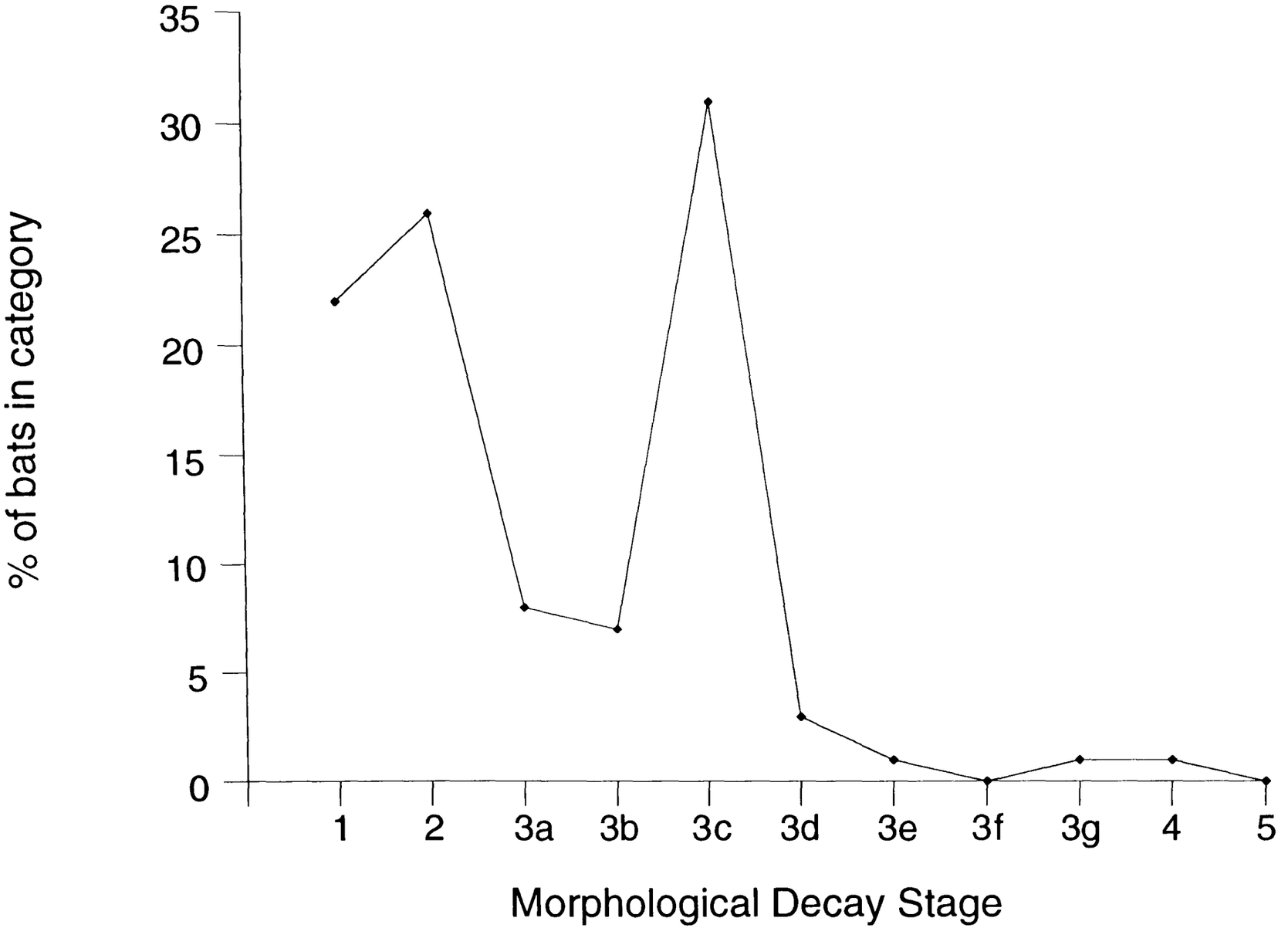


FIGURE 7.4 An unidentified bat (HLMD Me 7069) from Grube Messel. The specimen shows a "mushy" skeleton. The fragile bones within the centre of the body, i.e. the pelvis, ribs, vertebrae, scapula, have all been dissolved by diagenetic pore waters. The outline of the soft tissue is preserved.

Chapter Eight
The Taphonomy of Pterosaur Wing Membranes

8a. Introduction

A comprehensive review of the taphonomy of pterosaurs is beyond the scope of this thesis. However, some experiments on modern analogous tissues were carried out to investigate the taphonomy of pterosaur wing membranes. The aim of these experiments was to clarify the debate about the fibres within the wing (see below for an account of this controversy).

Pterosaurs have been recovered from sediments representing diverse palaeo-environments. There are some localities from which a large number of specimens are available for taphonomic analysis, primarily the Solnhofen Lithographic Limestone. Observations of the pterosaurs from this locality show that they behave taphonomically in a similar fashion to *Archaeopteryx* (Chapter 6d). Preliminary observations show that specimens follow a similar morphological decay sequence to that of birds (Chapter 2b4), the only major differences being that the tail of rhamphorhynchoids resists disarticulation due to the "stiffening rods" (elongated chevron bones) along the outside of the caudal vertebrae, and that the femur/pelvis articulation decays relatively earlier than in birds.

One question that I attempted to answer whilst conducting experiments on the taphonomy of birds was, how did the wing membranes of pterosaurs preserve?

The wing membranes of pterosaurs have been known for over 100 years (Marsh, 1882; Zittel, 1882). In subsequent years nearly eighty specimens of pterosaurs with traces of wings have been discovered (Padian and Rayner, 1993, and references therein). The interpretation of the structures within the wing membranes have been the subject of intense debate (e.g. Pennycuick, 1988; Martill and Unwin, 1989; Padian and Rayner, 1993). These structures have been termed Aktinofibrillen by Wellnhofer (1987) (structural fibers of Padian and Rayner, 1993). Whether these structures are fibres still remains to be proven but most researchers are now certain that they do exist. Most of the research on the fibres has analysed their aerodynamical/mechanical function and position within the membrane.

8b. Method.

To investigate the experimental taphonomy of the wing membrane analogous structures must be found within the modern environment. The first,

obvious choice would be the patagium, of bats as this is the only modern membrane used for active flight; unfortunately the lack of specimens available excluded this possibility. An alternative structure (which was more readily available to me when I was conducting these experiments) is the throat pouch of pelicans (*Pelicanus occidentalis*, Brown Pelican). The throat pouch contains similar structures (e.g. *Stratum corneum* and *Stratum vasculosum*) to those described in the exceptionally preserved pterosaur wing membrane from the Lower Cretaceous of Brazil (Martill and Unwin, 1989). The throat pouch of pelicans also contains a network of elastin fibres which mimic the effect of the aktinofibrillen (the aktinofibrillen may have been composed of one or more of three biological structural materials: elastin, keratin or collagen (pers. comm. D. Unwin)).

The throat pouch experiment was carried out in the freshwater environment as used for birds and bats (Chapter 2). The experimental method (Chapter 2b1) was modified as follows. Six sections of throat pouch (3cm^2 in size) were prepared by dissection. Six plastic dishes (15cm in diameter) were buried 6cm into the sediment of the field site. A piece of throat pouch was placed on the sediment in the centre of the buried dish. A wire and plastic mesh (like those described in Chapter 2b1) was placed over the dish. This prevented scavenger attack and also prevented the piece of throat pouch being transported away and lost. One specimen was collected at 1, 4, 7, 11, 28 and 56 days after the start of the experiment. These specimens were removed from the sediment and prepared for SEM study by the HMDS technique (Nation, 1983).

8c. Results

The pieces of pouch decayed slowly. Even after 56 days decay a very thin remnant remained. This is in contrast to the rapidity of soft tissue decay in birds in the same environment (Chapter 2b6). This may reflect the deeper burial of the pouch pieces which allowed only anoxic decay to occur. The decay experiments show that the *stratum vasculosum* of the pelican pouch decays rapidly (within 56 days) allowing the elastin network to be exposed at the surface (Figures 8.1, 8.2 and 8.3). Elastin fibres are recalcitrant and remain for up to 56 days even when only vestiges of the epithelium remain (Figure 8.3).

8d. Discussion

The wing membranes of pterosaurs from the Solnhofen Lithographic Limestone show irregular ridges (which have been interpreted as folds in the patagium, Padian and Rayner, 1993) and parallel 'fibres'. The taphonomy of

these wing membranes appears to be identical to that of the feather impressions of the skeletal *Archaeopteryx* specimens (Chapter 5). The preservation depends upon formation of an early diagenetic fabric (by bacterial action) which then takes an impression of the decaying wing membrane (see Chapter 5 for a full description). This therefore implies that the fibres must either have been at the surface (Padian and Rayner, 1993) or, if they were within the patagium, decay must have proceeded sufficiently to allow these structures to approach the surface of the membrane. The rapid decay of the stratum vasculosum in the pelican pouch indicates that the fibres of pterosaurs may have been within the wing membrane (this has been confirmed by further SEM investigation of the exceptionally preserved membrane described by Martill and Unwin (1989) (D. Martill and D. Unwin, pers. comm., 1993 and 1994).

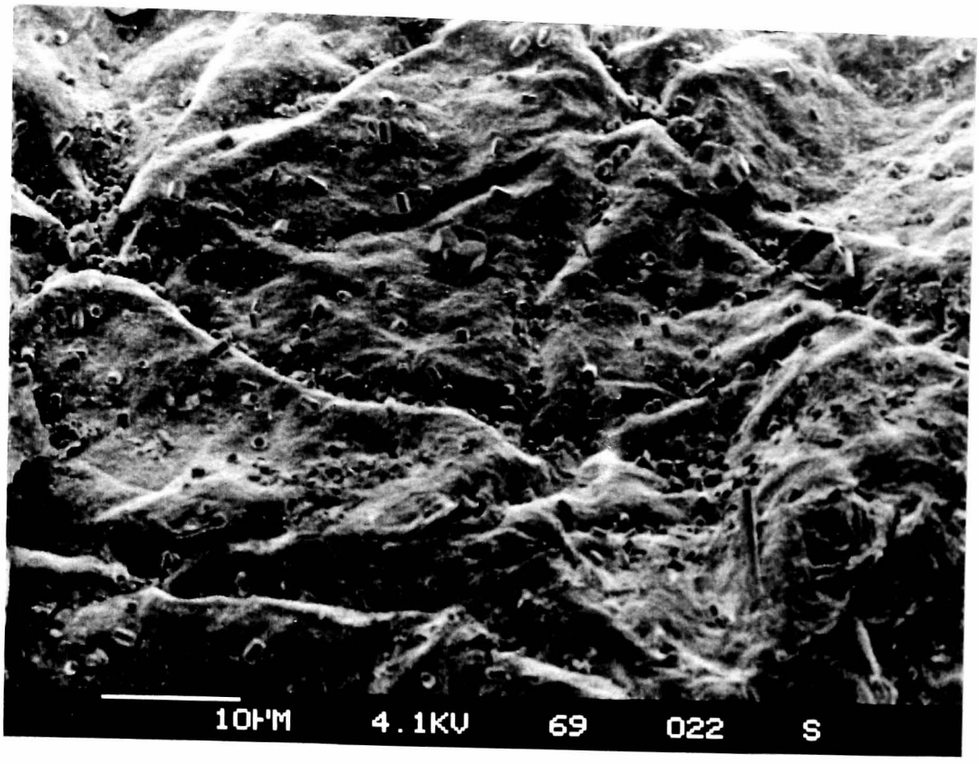
Elastin fibres are recalcitrant and remain for up to 56 days even when only vestiges of the epithelium remain (Figure 8.3). Thus decay of the pterosaur wing membranes of Solnhofen is likely to have been halted (probably by lithification) between 4 days (when the membrane has decayed enough to allow the fibres to be near the surface of the skin) and 56 days (when the recalcitrant fibres are starting to lose their integrity).

8e. Conclusions

These taphonomy experiments have provided further evidence that the fibres are *within* the wing membrane; they also show that decay occurred within the Solnhofen Lithographic Limestone pterosaurs so that wing planiforms should be regarded with suspicion. The experiments have not, however, determined the nature of the biological material that forms the fibres.

FIGURE 8.1 The surface epithelium of an undecayed pelican pouch showing polygonal wrinkles. The crystals on the surface are caused by the HMDS fixing process.

FIGURE 8.2 The surface of a pelican pouch after one day of decay. The surface has been covered by bacteria and sediment adheres to the bacterial glycocalyx. It is envisaged that this process caused the early diagenesis in Solnhofen which preserved the outline of the pterosaur membrane.


10µM 4.1KV 69 022 S

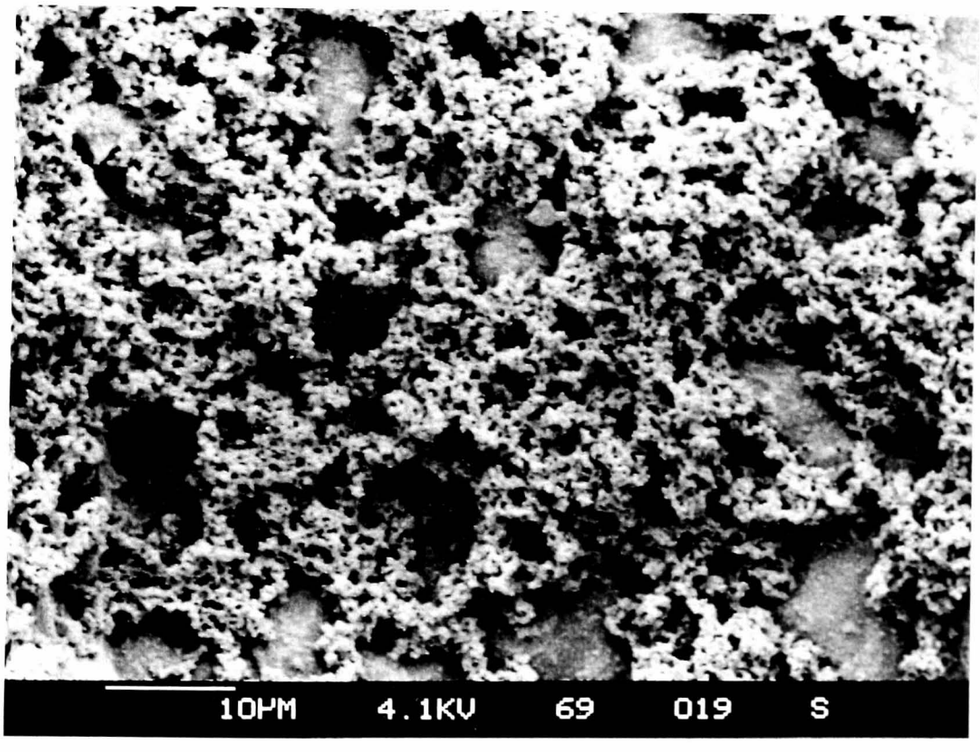
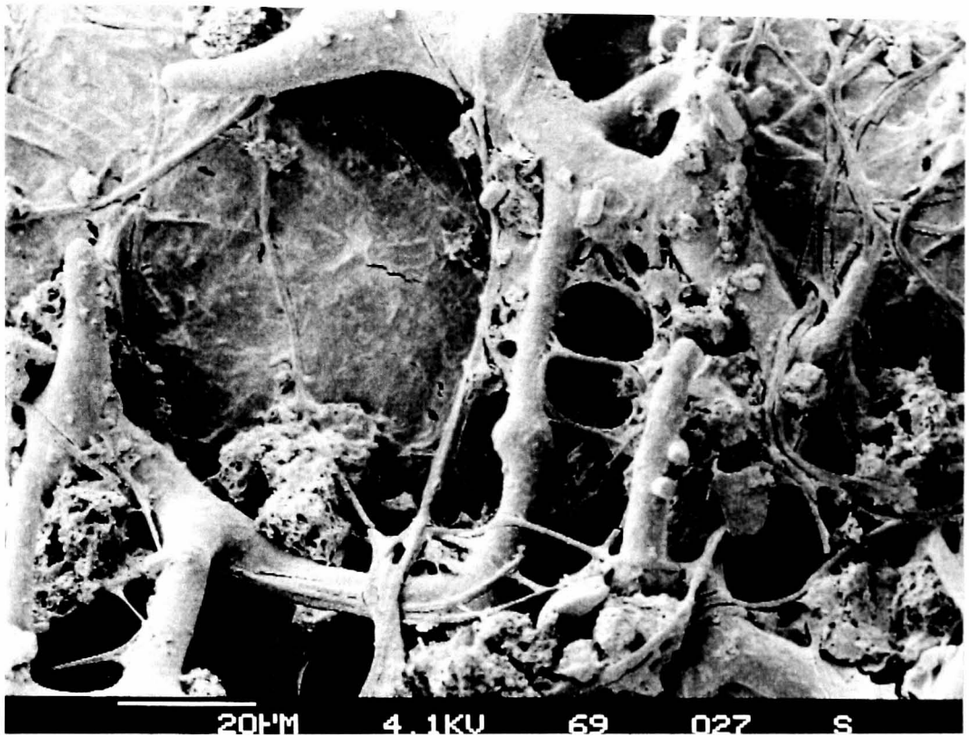

10µM 4.1KV 69 019 S

FIGURE 8.3 A pelican pouch after 56 days of decay. The integrity of the internal structure has been lost. Only the recalcitrant elastin fibres remain undecayed.


20UM
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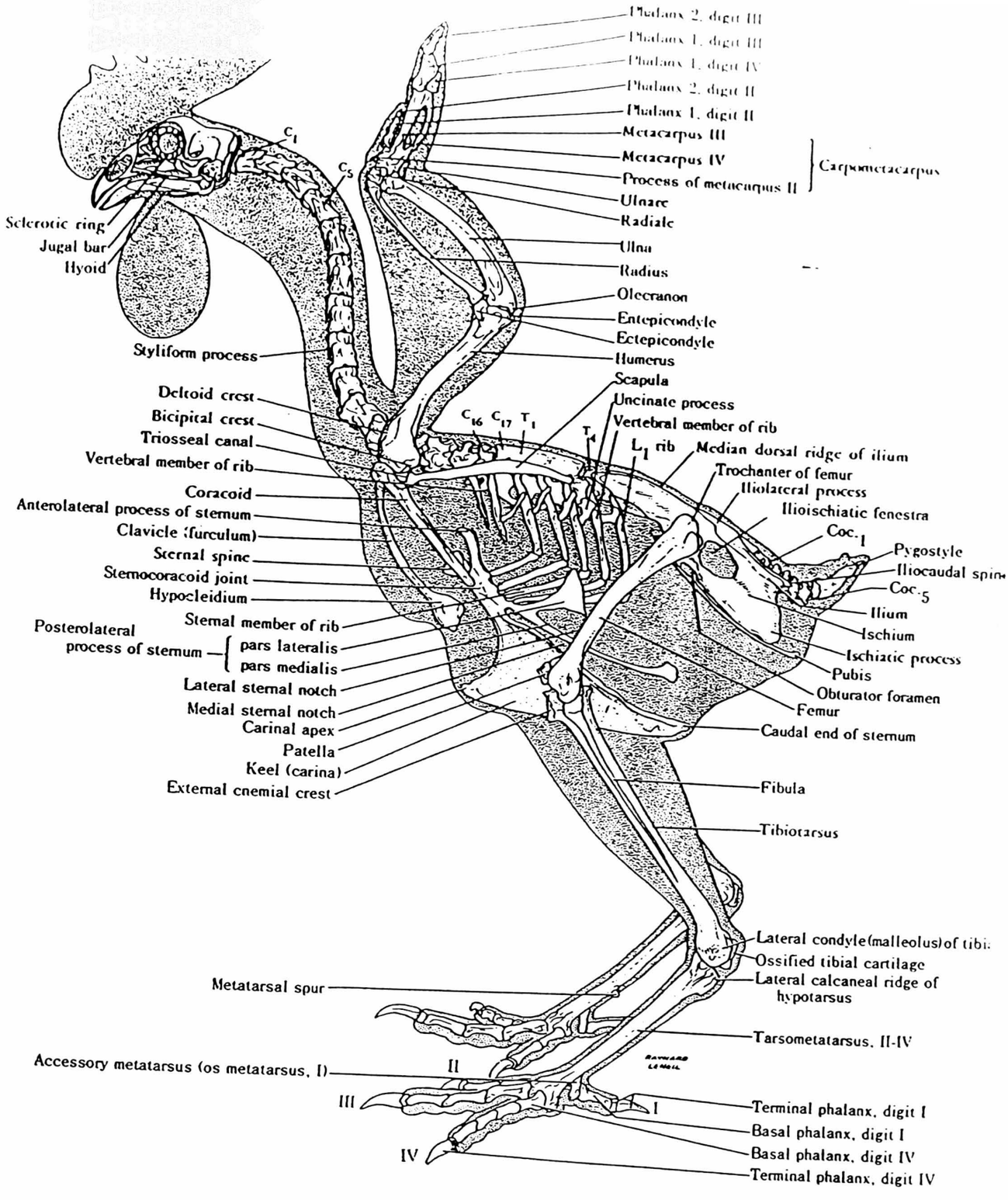
69
027
S

Chapter Nine
Conclusions

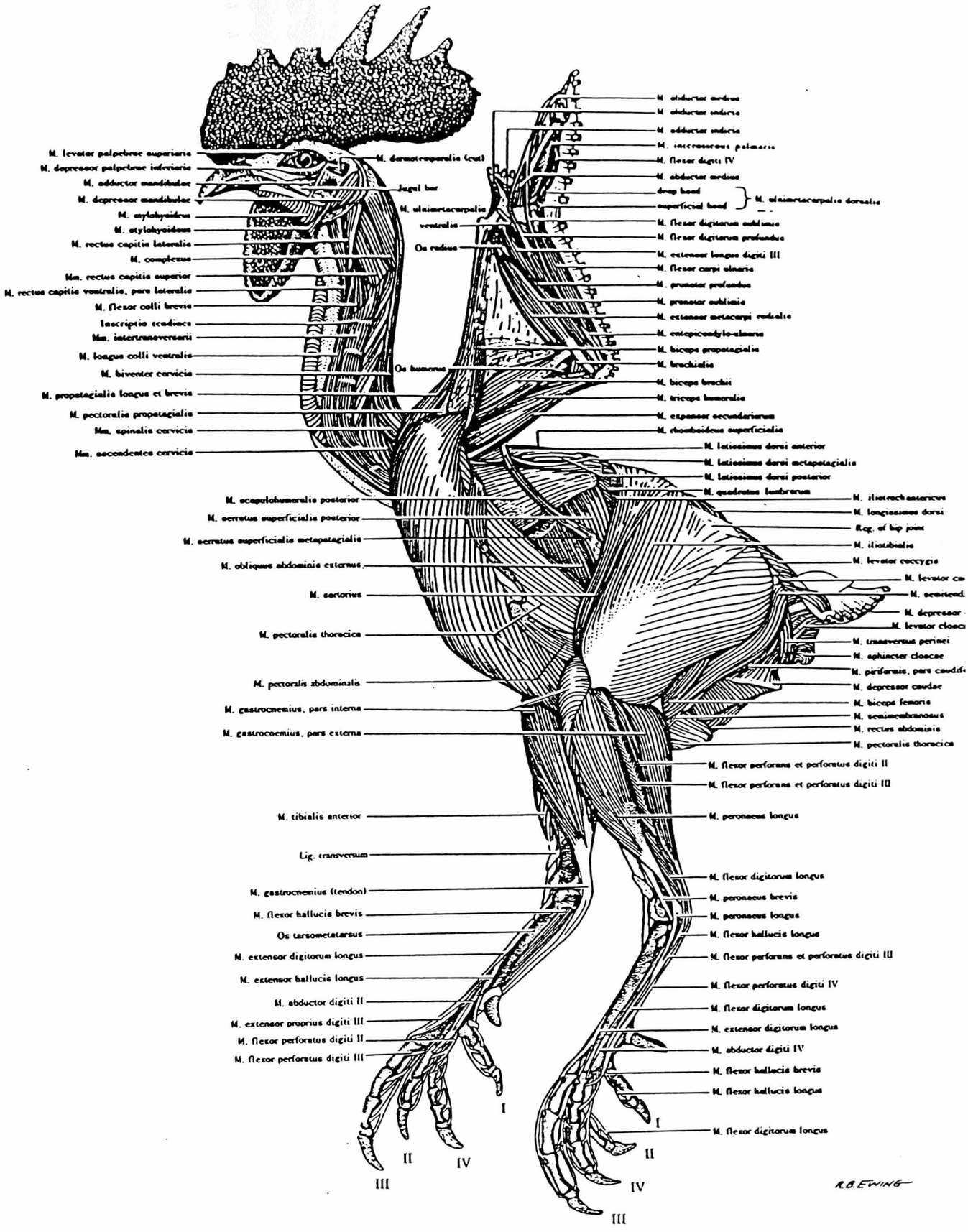
This research supports the following major conclusions:

- The rate of decay of birds is exponential (definable by equation 2.2).
- Decay remains exponential even when scavenging occurs.
- The following factors affect the rate of decay: predation/scavenging, temperature, rate of burial, transport, and anoxia.
- Birds disarticulate following a definable morphological decay sequence.
- This sequence can be observed in the fossil record.
- This decay sequence allows factors that enhance/inhibit decay within the fossil record to be defined.
- These enhancement/inhibiting factors are: transport, anoxia, scavenging, rate of burial, and temperature.
- Bird bones are bioeroded by endolithic cyanobacteria and algae. The bioerosion observed mimics damage caused by transport.
- The causes of bird mortality (predation, disease, senility, accident, starvation/dehydration) are difficult to observe in fossil material.
- The biostratinomy results of Napawongse (1981) and the re-interpretation of them can be applied to modern and fossil examples.
- The decay of birds in the natural environment can be reproduced in experiments.
- Fossil feathers are not uncommon in Tertiary sediments.
- Fossil feathers are preserved by bacterial action.
- Fossil bacterial glycocalyces have been observed replicating feather outlines.
- The "organic" traces of fossil feathers are diagenetically altered bacterial glycocalyces.
- The fossil record of birds is not depauperate.
- The fossil record of birds is biased.
- This bias favours aquatic and marine birds whereas, terrestrial and coastal birds are underrepresented.
- The similarities of structures in birds, pterosaurs and bats is sufficient to result in similar taphonomic pathways.
- The pterosaur wing membrane contains fibres inside the membrane.
- The wing membranes of Solnhofen Lithographic Limestone pterosaurs had decayed so wing planiforms used in aerodynamical reconstructions should be regarded with suspicion.



APPENDIX 1: Generalised Avian Anatomy

Figure A1.1 Lateral view of the skeleton of a Chicken. Abbreviations: C., cervical vertebra; Coc., caudal vertebra; L., lumbar vertebra; T., thoracic vertebra. From Lucas and Stettenheim (1972).



APPENDIX 1: Generalised Avian Anatomy

Figure A2.2 Lateral view of the myology of a Chicken. Abbreviations: Lig., Ligamentum; M (m)., Musculus (i); Reg., Region. From Lucas and Stettenheim (1972).

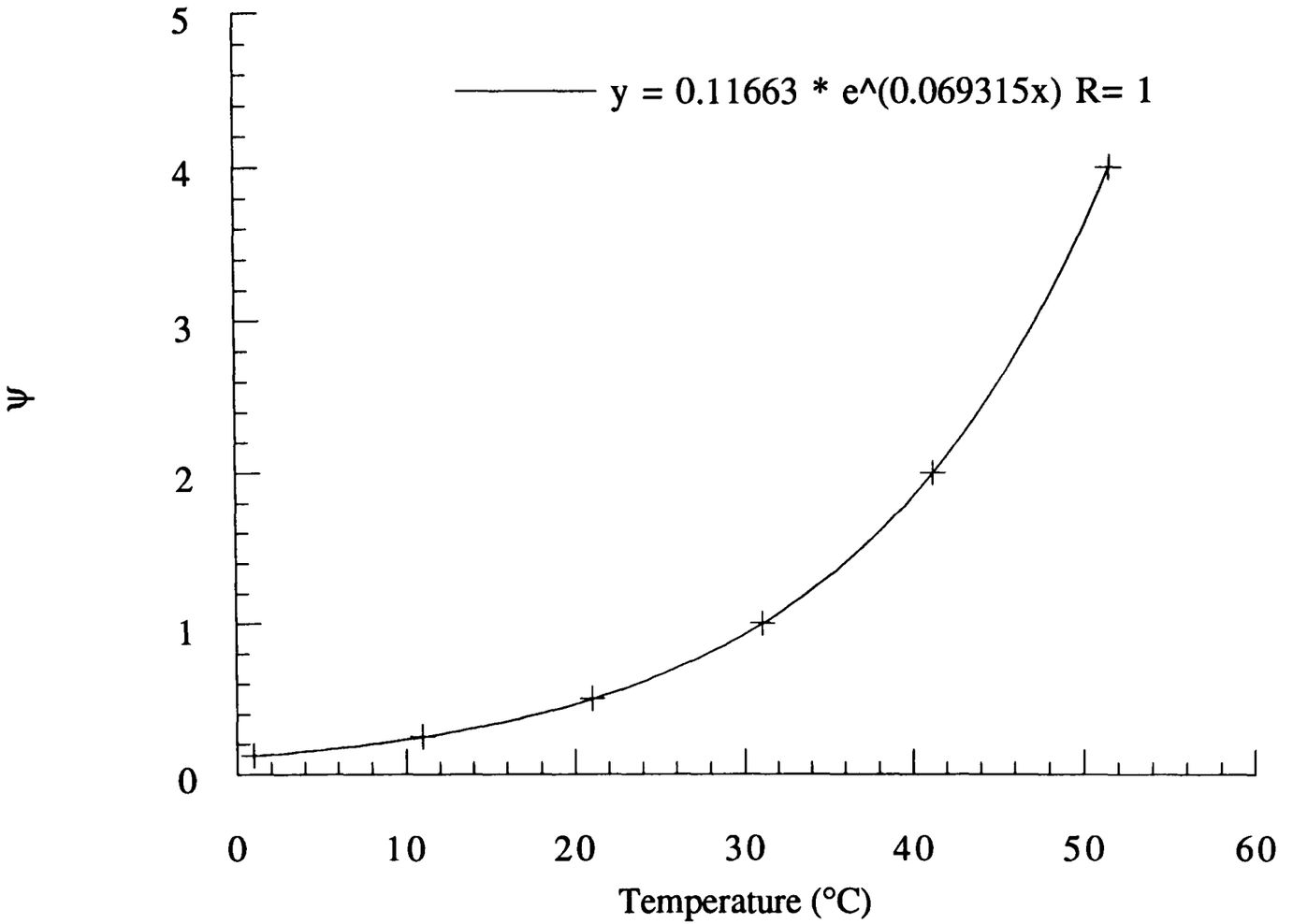
APPENDIX 2: The relationship between the Temperature constant (y) and Temperature

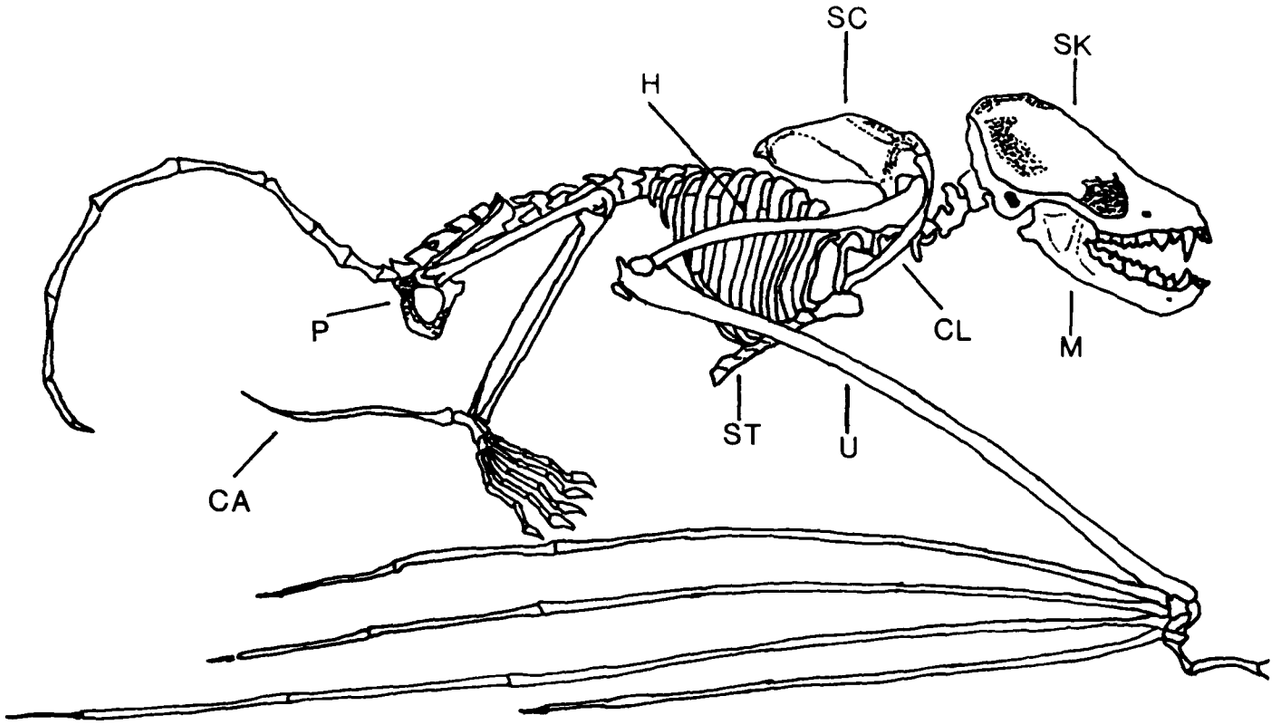
The relationship between y and temperature is expressed in Figure A.2.1. The equation for the graph was calculated by the Kalaeidograph package on the Apple Macintosh. By using this equation and substituting temperature into the X value and obtaining the y value (=Y value) the following table (Table A.1) was produced.

Temp. °C	y	Temp. °C	y	Temp. °C	y
-11	0.054	10	0.233	31	1.000
-10	0.058	11	0.250	32	1.072
-9	0.063	12	0.268	33	1.149
-8	0.067	13	0.287	34	1.231
-7	0.072	14	0.308	35	1.320
-6	0.077	15	0.330	36	1.414
-5	0.082	16	0.354	37	1.516
-4	0.088	17	0.379	38	1.625
-3	0.095	18	0.406	39	1.741
-2	0.102	19	0.435	40	1.866
-1	0.109	20	0.467	41	2.000
0	0.117	21	0.500	42	2.052
1	0.125	22	0.536	43	2.297
2	0.134	23	0.574	44	2.462
3	0.144	24	0.616	45	2.639
4	0.154	25	0.660	46	2.828
5	0.165	26	0.707	47	3.031
6	0.177	27	0.758	48	3.249
7	0.189	28	0.812	49	3.482
8	0.203	29	0.871	50	3.732
9	0.218	30	0.933	51	4.000

TABLE A.1 **Values of y for corresponding temperature values from -11°C to 51°C.**

Figure A2.1 Graph of temperature constant versus temperature





APPENDIX 3: Chiropteran Skeletal Anatomy

Figure A3 Lateral view of the skeleton of a Chiropteran. Abbreviations: SK = skull, SC = scapula, M = mandible, CL = clavicle, H = humerus, U = ulna, ST = sternum, P = pelvis, CA = calcar.

APPENDIX 4: Tabulated data of % weight loss for the eight experimental categories

Day	FLP	FSP	FLUP	FSUP	SLP	SSP	SLUP	SSUP
0	100	100	100	100	100	100	100	100
1	98	85	85	80	98	91	95	80
4	89	55	22	41	79	42	0	7
7	33	22	19	39	25	15	0	0
11	32	11	9	1	0	29	0	0
28	8	4	8	0	5	4	10	0
56	7	0	9	0	4	5	9	0
70	0	0	6	0	0	3	0	0

KEY (also see Table 2.3)

FLP = Freshwater, Large Protected

FSP = Freshwater, Small Protected

FLUP = Freshwater, Large Unprotected

FSUP = Freshwater, Small Unprotected

SLP = Seawater, Large Protected

SSP = Seawater, Small Protected

SLUP = Seawater, Large Unprotected

SSUP = Seawater, Small Unprotected

APPENDIX 5: Institutions and collections examined and abbreviations

Natural History Museum, London, England (BMNH)

All fossil bird material examined. This includes collections from; Green River Formation, La Meseta Formation, the London *Archaeopteryx* specimen, and the fossil feather collection.

Smithsonian Institution, Washington D.C., U.S.A (USNM)

All fossil bird material examined. This includes collections from: Green River Formation (including specimens from other instituions including Geological Survey of Alabama (GSATC) and Geological Museum of the University of Wyoming (GMUW)), Rancho La Brea, La Meseta Formation, and the fossil feather collection.

Hessiches Landesmuseum, Darmstadt, Germany (HLMD)

Complete Grube Messel fossil bird, bat, and feather collections.

Field Museum of Natural History, Chicago, U.S.A. (FMNH)

Complete Green River Formation fossil bird and feather collections.

APPENDIX 6: *Pro forma* for recording taphonomic data from fossil birds within Lagerstätten.

Repository	
Specimen No.	
Identification/Ecological Type	
Locality	
Age	
Formation	
Zone	
Sediment Lithology	
Pyrite Preservation	
Concretionary Cementation	
Compactional Deformation	
Phosphatisation	
Replacement	
Current/Wave Orientation	
Death Marks	
Landing Marks	
Soft Tissue Preservation	
Feather Preservation	
Disarticulation Index	
Original Habitat	
Comments	

Appendix 7: Morphological Decay Stages Data

The 64 experimental specimens from the Florida decay experiments (Chapter 2) were examined daily (for days 0 to 10, days 19 to 30, days 47, 56 and 70). On these visits the decay of the specimens was recorded by noting which joints had disarticulated, i.e. head from cervical vertebrae etc. By ordering the disarticulating joints based upon their frequency (i.e. the total number of these joints disarticulating divided by the numbers of these joints in a skeleton) the morphological decay sequence was created. It may be noted that the numbers in all the categories add up to more than 64 (the total number of specimens). This is because most specimens were observed over a period of time and it was possible to observe specimens decaying further (and consequently be able to be placed in several morphological stages).

Morphological Decay Stage	1+2	3a	3b	3c	3d	3e	3f	3g	4	5
Nos. of Specimens	64	29	24	20	18	17	15	12	11	4
Average time to reach stage (days)	1-3	3	3	3	3	3	12	34	40	52

Appendix 8: Data for Lagerstätten Case Studies

Fossil Birds from Green River Fm. (Eocene), Wyoming

Name	Repository and Specimen No.	Feathers	Soft Tissues	Morphological Decay Stage
Limnofregata azygosternon	USNM 22753	Yes	Body Area	3c
Limnofregata azygosternon	USNM 243766	No	No	5
?	USNM 253427	No	No	3b
?	USNM 299821	No	No	3b
Eobucco cf. *brodkorbi*	USNM 424077	?	?	2
Pseudocrypturus cercanaxius	USNM 336103	No	No	3a
?	USNM 336261	No	No	3c
?	USNM 336263	No	No	3d
?	USNM 336264	No	No	3b
?	USNM 336268	No	No	2
?	USNM 336269	No	No	3b
?	USNM 336270	No	No	3g
?	USNM 336271	No	No	3d
?	USNM 336272	No	No	3g
?	USNM 336273	No	No	3c
?	USNM 336275	No	No	3c
?	USNM 336277	No	No	3b
Prefica nivea	USNM 336278	No	No	3e
?	USNM 336280	No	No	3b
?	USNM 336281	No	No	3d
?	USNM 336282	No	No	3f
?	USNM 336283	No	No	3d
?	USNM 336284	No	No	2

Name	Repository and Specimen No.	Feathers	Soft Tissues	Morphological Decay Stage
?	USNM 336377	Yes	Body Area	1
?	USNM ?	No	No	3f
?	USNM ?	No	No	3a
Pseudocrypturus cercanaxius	USNM acc. 424078	No	No	2
?	USNM ?	No	No	3d
?	FMNH PA 345	No	No	3c
?	FMNH PA 346	No	No	3c
?	FMNH PA 607	No	No	3c
?	FMNH PA 608	No	Tracheal rings	1
?	FMNH PA 609	No	No	2
?	FMNH PA 610	No	No	3a
?	FMNH PA 611	No	No	3c
?	BHI 207	No	No	2
Primobucco olsoni	GSATC 217	Yes	Ubiquitous	1
Neanis schucherti	YPM 1233	Yes	No	3c
Limnofregata azygosternon	UW 6919	No	No	3c
Primobucco kistneri	UW V690103196	No	No	3a
?	UW V801013299	No	No	3a
?	UW V8010220312	No	No	2

Fossil Birds from Messel (Eocene), Germany

Name	Repository and Specimen No.	Feathers	Soft Tissues	Morphological Decay Stage
?	HLMD Me 10204	Yes	Body area	3a
?	HLMD Me 7623	No	No	3b
?	HLMD Me 9793	No	No	3b
?	HLMD Me 7607	No	No	3c
?	HLMD Me 7583	No	No	3b
?	HLMD Me 10206	Yes	Body area	3b
?	HLMD Me 7999	No	No	3c
?	HLMD Me 9800	No	No	3a
?	HLMD Me 7626	No	No	3a
?	HLMD Me 7627	No	No	3c
?	HLMD Me 7947	No	No	3b
?	HLMD Me 9797	No	No	2
?	HLMD Me 8872	No	No	2
?	HLMD Me 7601	No	No	3c
?	HLMD Me 10472	Yes	Body area	2
?	HLMD Me ?	No	Wing and Body area	2
?	HLMD Me 7618	No	No	3b
?	HLMD Me 7622	Yes	Wing and Body area	2
?	HLMD Me 9779	No	No	3c
?	HLMD 7946Me	No	No	3b
?	HLMD Me 7621	No	No	3b
Messelornis cristata	HLMD Me 7408	No	No	3b
?	HLMD Me 9748	Yes	Body area	2
?	HLMD Me 7629	Yes	Body area	3c

Name	Repository and Specimen No.	Feathers	Soft Tissues	Morphological Decay Stage
?	HLMD Me 10478	Yes	No	2
?	HLMD Me 5470	No	No	3b
?	HLMD Me ?	No	No	2
?	HLMD Me ?	?	?	2
?	HLMD Me ?	No	No	2
?	HLMD Me ?	No	No	3c
?	HLMD Me ?	No	No	3a
?	HLMD Me 7471	No	No	3b
?	HLMD Me 7472	No	No	2
?	HLMD Me 7325	No	No	5
?	HLMD Me ?	No	No	3b
?	HLMD Me ?	No	No	3b
?	HLMD Me ?	No	No	3a
?	HLMD Me ?	No	No	3a
?	HLMD Me 7347	No	No	2
?	HLMD Me ?	No	No	2
'Dave'	HLMD Me ?	No	No	2
Ralliformis sp.	HLMD Me ?	No	No	3c
?	HLMD Me ?	No	No	2
?	HLMD Me ?	No	No	2
?	HLMD Me 8082	?	Wing area	3c
?	HLMD Me 8085	No	No	3c
?	HLMD Me 7501	Yes	Body area	3a
?	HLMD Me 7808	Yes	Eye socket	3d
?	HLMD Me 8100	No	No	3a
?	HLMD Me ?	No	Wing area	3e
?	HLMD Me ?	No	No	2
?	HLMD Me ?	Yes	No	3c
? *Rhynchaeïtes* sp.	HLMD Me ?	No	No	2
Rhynchaeïtes sp.	HLMD Me ?	No	No	2
?	HLMD Me ?	No	No	2
?	HLMD Me ?	No	No	3a
?	HLMD Me 8969	Yes	Body area	1
?	HLMD Me 7557	No	No	3c

Name	Repository and Specimen No.	Feathers	Soft Tissues	Morphological Decay Stage
?	HLMD Me 7561	No	No	2
?	HLMD Me 7038	No	No	3a
?	HLMD Me 5471	No	No	3a
?	HLMD Me 7474	Yes	Body area	1
?	HLMD Me 7950	No	No	3a
?	HLMD Me 7570 + 1	No	No	2
?	HLMD Me 7471	No	No	2
?	HLMD Me 5472	No	No	3a
?	HLMD Me 7235	No	Body area	3a
?	HLMD Me 7268	Yes	No	3c
?	HLMD Me 7119	No	No	3c
?	HLMD Me 5469	No	Tracheal rings	3a
?	HLMD Me 7565	No	No	4
?	HLMD Me 7120	No	No	3a
?	HLMD Me ?	No	Body area	1
?	HLMD Me 10479	No	No	2
?	HLMD Me 8083	No	No	3c
?	HLMD Me 9763	No	No	3f
?	HLMD Me 9764	No	Stomach contents	3a
?	HLMD Me 7560	No	No	3a
?	HLMD Me 7563	No	No	3e
?	HLMD Me 7567	No	No	3d
?	HLMD Me 7566	Yes	No	3a
?	HLMD Me 7562	No	No	3b

Name	Repository and Specimen No.	Feathers	Soft Tissues	Morphological Decay Stage
?	HLMD Me 7572	No	Stomach area	3d
?	HLMD Me 7568	No	Body area	3d
?	HLMD Me 10474	Yes	Ubiquitous	1
Aegialornis szarskii	HLMD Me 7598	Yes	No	3d
?	HLMD Me 8972	No	Ubiquitous	1
?	HLMD Me 7587	No	Body area	3a
?	HLMD Me 9725	No	Body area	3a
?	HLMD Me 9045	No	Body area	3a
?	HLMD Me 7993	No	No	3f
Palaeotis weigelti	HLMD Me 771	No	No	2
?	HLMD Me 7616	Yes	No	3c
?	HLMD Me 7961	No	Skull and Body area	3b
Messelornis cristata	HLMD Me 9048	No	Body area	1
?	HLMD Me 9109	?	No	3c
?	HLMD Me 9507	No	No	3b
?	HLMD Me 9056	No	No	3b
?	HLMD Me 9047	Yes	Body area	1
?	HLMD Me ?	No	No	3a
?	HLMD Me ?	No	No	3a
?	HLMD Me ?	No	No	3c
?	HLMD Me ?	Yes	No	3c
?	HLMD Me ?	No	No	3b
?	HLMD Me ?	No	No	2
?	HLMD Me ?	No	No	3c
?	HLMD Me 7473	Yes	Ubiquitous	1
Messelornis cristata	HLMD Me 7475	No	Yes	1
Diatryma cf. steini	HLMD Me 6116	No	No	4

Name	Repository and Specimen No.	Feathers	Soft Tissues	Morphological Decay Stage
Rhynchaeïtes messelensis	HLMD Me 7470	No	No	3a
?	HLMD Me ?	No	No	3a
?	HLMD Me ?	No	No	3a
?	HLMD Me ?	No	No	3a
?	HLMD Me ?	No	No	3c
?	HLMD Me ?	No	No	2
? *Aegialornis*	HLMD Me ?	No	No	3b
?	HLMD Me ?	No	No	2
Rhynchaeïtes messelensis	HLMD Me ?	No	No	2
?	HLMD Me ?	No	No	3c
?	HLMD Me ?	No	No	2
?	HLMD Me ?	No	No	3c
Psittaciform ?	HLMD Me ?	No	No	3c
?	HLMD Me ?	No	No	2
?	HLMD Me ?	No	No	2

Appendix 9. Fossil Bats from Messel (Eocene), Germany

Name	Repository and Specimen No.	Soft Tissues	Morphological Decay Stage
Palaeochiropteryx tupaiodon	HLMD Me 26	No	3a
Palaeochiropteryx tupaiodon	HLMD Me 39	No	2
Palaeochiropteryx tupaiodon	HLMD Me 22	No	2
Palaeochiropteryx tupaiodon	HLMD Me 38	No	2
Palaeochiropteryx tupaiodon	HLMD Me 19	No	2
Palaeochiropteryx tupaiodon	HLMD Me 36	No	2
Archaeonycteris sp.	HLMD Me 14	No	3a
Palaeochiropteryx tupaiodon	HLMD Me 35	No	2
Palaeochiropteryx tupaiodon	HLMD Me 18	No	3e
Palaeochiropteryx tupaiodon	HLMD Me 25	No	2
Palaeochiropteryx tupaiodon	HLMD Me 37	No	2
Palaeochiropteryx tupaiodon	HLMD Me 40	No	3c
Palaeochiropteryx tupaiodon	HLMD Me 24	Body area	1
Palaeochiropteryx tupaiodon	HLMD Me 23	No	3a
Palaeochiropteryx tupaiodon	HLMD Me 17	No	3d
Archaeonycteris trigonodon	HLMD Me 33	No	3a
Archaeonycteris trigonodon	HLMD Me 15	No	2
?	HLMD Me 96	No	3c
Palaeochiropteryx tupaiodon	HLMD Me 27	No	3c
Palaeochiropteryx spiegeli	HLMD Me 32	No	2
?	HLMD Me 7558	Stomach contents	1
?	HLMD Me 7498	Body area	3a
?	HLMD Me 8873	Body and Wing area	1
?	HLMD Me 9113	Body area	1
?	HLMD Me 9112	Body area	1
?	HLMD Me 8973	Wing area	3c
?	HLMD Me 7628	Body area	1
?	HLMD Me 7069	Body area	1

Name	Repository and Specimen No.	Soft Tissues	Morphological Decay Stage
?	HLMD Me 9115	No	3c
Archaeonycteris sp.	HLMD Me 34	No	3c
Palaeochiropteryx spiegeli	HLMD Me 31	No	3c
Palaeochiropteryx spiegeli	HLMD Me 29	No	2
Archaeonycteris sp.	HLMD Me 13	No	3c
Palaeochiropteryx spiegeli	HLMD Me 30	No	2
?	HLMD Me 7559	Wing area	3c
?	HLMD Me 9726	Stomach contents	1
Palaeochiropteryx tupaiodon	HLMD Me 28	No	3c
Palaeochiropteryx tupaiodon	HLMD Me 21	No	2
Palaeochiropteryx tupaiodon	HLMD Me 153	No	2
Palaeochiropteryx tupaiodon	HLMD Me 151	No	2
?	HLMD Me 7276	No	2
?	HLMD Me 7219	Wing and Body area	3c
Palaeochiropteryx tupaiodon	HLMD Me 44	No	3c
Palaeochiropteryx tupaiodon	HLMD Me 45	No	3c
?	HLMD Me 7177	No	3c
?	HLMD Me 7069	Wing and Body area	1
Palaeochiropteryx spiegeli	HLMD Me 152	No	3c
?	HLMD Me 7290	Wing and Body area	3b
Palaeochiropteryx tupaiodon	HLMD Me 20	No	3c
Palaeochiropteryx tupaiodon	HLMD Me 150	No	2
Palaeochiropteryx tupaiodon	HLMD Me 690	No	2
?	HLMD Me 7944	Body area	4
?	HLMD Me 7998	Body area	3c
?	HLMD Me 9781	Body area	3c
?	HLMD Me 7613	Body area	3a
?	HLMD Me 8871	Body area	3c
Palaeochiropteryx tupaiodon	HLMD Me 9017	Body area	1
?	HLMD Me 7605	Wing area	3c
?	HLMD Me 7619	Stomach contents	3d
?	HLMD Me 7941	No	3c
?	HLMD Me 9792	No	3g

Name	Repository and Specimen No.	Soft Tissues	Morphological Decay Stage
?	HLMD Me 10466	Head and Thorax area	3b
?	HLMD Me 10463	Wing and Body area	1
?	HLMD Me 10476	Wing and Stomach contents	3b
?	HLMD Me 10465	Stomach contents	1
Palaeochiropteryx sp.	HLMD Me 7620	Stomach contents	1
?	HLMD Me 7630	Body and Stomach contents	1
Hassianycteris magna	HLMD Me 7539	Wing and Stomach contents	1
Hassianycteris messelensis	HLMD Me 7480	Stomach contents	3b

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